A TEXTBOOK
OF
GENERAL BOTANY

BOTANY TEXTS

ELEMENTS OF BOTANY

By RICHARD M. HOLMAN, Associate Professor of Botany in the College of Letters and Science of the University of California; and WILFRED W. ROBBINS,. Professor of Botany in the College of Agriculture of the University of California. 380 pages. 5½ by 8½. 241 figures. Cloth.

TEXTBOOK OF GENERAL BOTANY

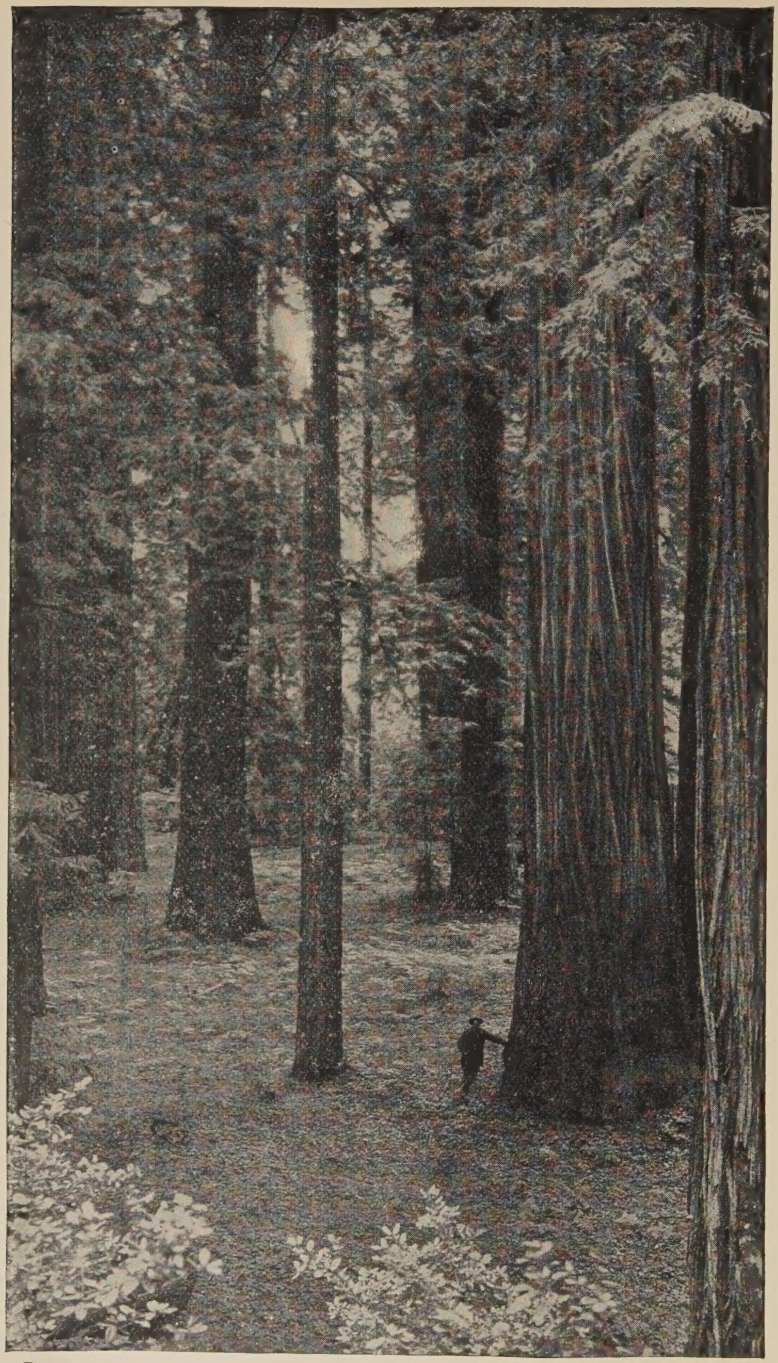
For Colleges and Universities. By RICHARD M. HOLMAN and WILFRED W. ROBBINS. Second Edition, 624 pages. 6 by 9. 415 figures. Cloth.

LABORATORY GUIDE FOR A COURSE IN GENERAL BOTANY

By LEE BONAR, RICHARD M. HOLMAN, and LUCILE ROUSH, all of the Department of Botany of the University of California. 106 pages. 6 by 9. Cloth.

PUBLISHED BY

JOHN WILEY & SONS



© *Woodbridge Metcalf.*

Frontispiece.

A FOREST OF REDWOOD

(*Sequoia sempervirens*)

A TEXTBOOK
OF
GENERAL BOTANY
FOR
COLLEGES AND UNIVERSITIES

BY

RICHARD M. HOLMAN

Associate Professor of Botany in the College of Letters and Science of the University of California

AND

WILFRED W. ROBBINS

Professor of Botany in the College of Agriculture of the University of California

SECOND EDITION

1928 PRINTING CORRECTED

NEW YORK

JOHN WILEY & SONS, INC.

LONDON: CHAPMAN & HALL, LIMITED

1928

Copyright, 1924, 1927
By RICHARD M. HOLMAN
AND
WILFRED W. ROBBINS

Printed in U. S. A.

PRESS OF
BRAUNWORTH & CO
BOOK MANUFACTURERS
BROOKLYN, N. Y.

10/28

PREFACE TO THE SECOND EDITION

In presenting the second edition of this textbook the authors can not refrain from expressing their appreciation of the favorable reception accorded the original edition and of the wide adoption of it, during the three years since its appearance, which has made possible this new edition.

Although a considerable number of changes have been made in the book, its organization and the method of treatment of the subject are not essentially different from those of the first edition. Before starting revision, criticisms and suggestions were invited from all those known to be using the book in their classes. The changes which have been made are for the most part based on the suggestions received in response to this invitation and upon the experience of the authors in the use of the book in their own classes. The principal changes are:

1. The introduction, in fine but easily legible print, into the first and second chapters, of brief statements of certain physical and chemical principles, acquaintance with which is prerequisite for an understanding of the fundamentals of plant physiology. This new feature seems justified in view of the fact that a large proportion of the students in courses in general botany have had no adequate instruction in chemistry or physics.

2. The placing of the chapter on "The Plant Body," previously called, "The Plant as a Whole," before the chapter on "The Cell" instead of after it as it was in the first edition.

3. The introduction at the end of "Part One" of a chapter entitled, "The Relation of the Plant to Its Environment" in place of the "Summary" chapter of the first edition. Considerable of the material of the "Summary" chapter is included, however, in the new chapter.

4. The introduction in the chapter on "The Spermatophyta" of an account of the principal tendencies in the evolution of the angiosperms, based on Clements' presentation of the Besseyan system.

5. Various changes throughout the text prompted by recent advances in botanical knowledge, particularly in histology and physiology.

6. The addition of more than fifty new illustrations and the redrawing, entirely or in part, of about the same number of the figures used in the first edition.

The authors gratefully acknowledge the helpful suggestions made and the assistance given by several of their associates in the botanical and agricultural departments of the University of California and by the following teachers in other colleges and universities: Howard C. Abbott, Rimo Bacigalupi, H. P. Barss, E. A. Bessey, Otis F. Curtis, Sarah L. Doubt, Clifford H. Farr, Margaret C. Ferguson, Robert Griggs, J. E. Kirkwood, P. A. Lehenbauer, H. E. McMinn, E. C. Miller, A. D. Oxley, Ethel G. Stiffler, W. I. Witterback and many others.

The authors are particularly indebted to Esther G. Holman for her criticism of the manuscript of the second edition and checking of the proof sheets.

Wilfred W. Robbins.
Richard M. Holman.

Berkeley, California,
October 7, 1927.

PREFACE TO THE FIRST EDITION

This book embodies the material of the lectures to the students in the two courses in General Botany given in the University of California. One of these courses, given at the Branch of the Agricultural College at Davis, is for agricultural students exclusively; the other, given at Berkeley, is attended by both agricultural and liberal arts students. Since there are frequent interchanges of students between the two institutions and since both courses serve as prerequisites for the same advanced courses, it is desirable that the two courses be essentially equivalent. During frequent conferences the authors of the present volume, who are responsible for the two courses, have on the basis of their experience in elementary botanical instruction in several universities and agricultural colleges found themselves in agreement upon the following points:

(1) That the agricultural student will profit more by a broad survey of the whole field of botany, in as far as that is possible or desirable in the elementary courses, than from a special course for agricultural students restricted to those aspects of botany which are capable of the most obvious and direct application to agriculture.

(2) That the general student in an elementary course in botany, no less than the agricultural student, will profit by having the subject related wherever possible to agricultural practices and problems, and by the use of economic plants for illustrative material in every case where they will serve the particular end as well as any other plants.

(3) That the results from such a course are likely to be more satisfactory if a relatively small number of forms and processes are discussed and studied with some degree of completeness than if the work is more superficial and extensive.

(4) That the usual procedure of presenting the subject matter of such a course largely by means of formal lectures leaves much to be desired and that a textbook which presented practically the whole content of the usual lectures on the fundamentals of general botany would result in better teaching, since it would make it possible for the instructor to devote more of his time and energy to the more effective work of recitation, conference and quiz.

(5) That, although an acquaintance with the activities of the plant, rather than with its structure, should be the primary aim of such a course, a knowledge of structure is essential to an intelligent understanding of function.

(6) That the text for such a course should be as fully illustrated as possible and that the usefulness of the illustrations would be greatly increased by direct labeling, wherever possible, of the parts of each structure illustrated.

We have endeavored to embody all of these considerations in the present text.

The text is designed for a year's course, the material covered by Part I to be taken up in one semester and by Part II in a second semester. However, Part I may be used alone. With the exception of the first and second, the Chapters of Part I have been so written that they may be taken up in any order desired by the instructor. If it is thought desirable to use Part II without taking up all the material in Part I, Chapters I and II may be used as introductory to Part II.

ACKNOWLEDGMENTS

Although the authors are indebted to a number of their colleagues, who have read certain chapters and made suggestions for their improvement, they accept sole responsibility for the contents of the book. Among those who have read certain chapters, especially those touching on their own particular field of study or interest, or who have made helpful suggestions during the preparation of the book are:

Professor C. B. Hutchison, Director of the Branch of the College of Agriculture at Davis, and Professor of Plant Breeding; Professors W. A. Setchell, N. L. Gardner, T. H. Goodspeed, and O. L. Sponsler, Dr. Lee Bonar, and Miss Lucile Roush of the Department of Botany of the University of California; Professors C. B. Lipman, P. B. Kennedy, R. E. Clausen, and J. P. Bennett of the Agricultural College of the University of California; Professor Francis Ramaley of the University of Colorado; and Professor D. H. Campbell of Stanford University.

The majority of the illustrations are original, and for their assistance in the preparation of these we wish especially to thank Miss Elisabeth Pratt, Miss Mildred Hollis, Miss Jane Mackie, and Mr. Charles Quibell.

In the case of illustrations which have been borrowed acknowledgment of the source has been made in the legend of each cut but we wish to express here our thanks to the following authors and publishers for their courtesy in permitting the use of figures: Professor A. H. H. Buller,

University of Manitoba; Professor D. H. Campbell, Stanford University; Professor Charles J. Chamberlain, University of Chicago; Professor John M. Coulter, University of Chicago; Professor C. C. Curtis, Columbia University; Professors Woodbridge Metcalf and E. Fritz, of the Division of Forestry, University of California; Professor C. S. Gager, Brooklyn Botanic Garden; Professors W. A. Setchell, W. L. Jepson, N. L. Gardner, and H. M. Hall, University of California; Professor John W. Harshberger, University of Pennsylvania; Professor E. C. Jeffrey, Harvard University; Professor William A. Locy, Northwestern University; Professor Edwin C. Miller, Kansas Agricultural College; Professor D. M. Mottier, University of Indiana; Professor John Percival, University College, Reading, England; Professor C. S. Sargent, Yale University; Professor Lester W. Sharp, Cornell University; Professor E. W. Sinnott, Connecticut Agricultural College; Professor W. C. Stevens, University of Kansas; Professor Warren P. Tufts, of the Division of Pomology, University of California; Professor J. E. Weaver, University of Nebraska; P. Blakiston's Son & Company, Figs. 46, 55, 56, 95, 100, 114, 120, 127, 172, 173, 174, 175, 176, 177, 178, 179, 181, 182, 183, 195, 198, 199, 200, 202, 209, Robbins' *Botany of Crop Plants;* Figs. 60, 68, 75, 136, Stevens' *Plant Anatomy;* Figs. 145, 146, 147, 148, Palladin's *Plant Physiology;* Figs. 165, 268, 279, Gager's *Fundamentals of Botany;* Fig. 258, Harshberger's *Mycology and Plant Pathology;* E. P. Dutton, Figs. 44, 45, 106, 357, 358, 367, 368, 369, Percival's *The Wheat Plant;* Ginn and Company, Figs. 123 and 188, H, from Bergen and Caldwell's *Practical Botany;* Henry Holt and Company, Figs. 12, 13, 14, Locy's *Biology and Its Makers;* Figs. 59, 156, 157, 186, 274, Kerner's *Natural History of Plants;* Figs. 74, 278, 323, 324, 355, Curtis' *Nature and Development of Plants;* The Macmillan Company, Fig. 54, Bailey's *Lessons with Plants;* Figs. 83, 107, 137, 138, 151, Haberlandt's *Plant Anatomy;* Fig. 180, Ganong's *A Textbook of General Botany;* Figs. 211, 237, C. Strasburger's *Textbook of Botany;* McGraw-Hill Company, Fig. 4, Sharp's *Cytology;* Fig. 262, Sinnott's *Botany-Principles and Problems;* University of Chicago Press, Fig. 109, Jeffrey's *The Anatomy of Woody Plants;* Figs. 162, 347, 348, 349, 350, 351, 354, Coulter and Chamberlain's *Morphology of Gymnosperms;* Fig. 263, Chamberlain's *Methods in Plant Histology.*

Richard M. Holman.
Wilfred W. Robbins.

Davis, California,
August 29, 1924.

CONTENTS

PAGE

PREFACE TO THE SECOND EDITION vii

PREFACE TO THE FIRST EDITION ix

PART I

THE STRUCTURE AND PHYSIOLOGY OF SEED-BEARING PLANTS

CHAPTER

I. INTRODUCTION 1

II. THE PLANT BODY 17

III. THE CELL 43

IV. THE STEM 87

V. THE ROOT 153

VI. THE LEAF 181

VII. THE FLOWER 234

VIII. FRUIT AND SEED 268

IX. RELATION OF THE PLANT TO ITS ENVIRONMENT 309

PART II

A SURVEY OF THE PLANT KINGDOM WITH PARTICULAR EMPHASIS UPON DEVELOPMENT, REPRODUCTION AND RELATIONSHIPS, INCLUDING ALSO A CHAPTER ON EVOLUTION AND HEREDITY

X. INTRODUCTION 335

XI. THE THALLOPHYTA-ALGAE 343

XII. THE THALLOPHYTA-FUNGI 391

XIII. THE BRYOPHYTA (LIVERWORTS AND MOSSES) 457

XIV. THE PTERIDOPHYTA (FERNS AND FERN ALLIES) 489

XV. THE SPERMATOPHYTA (SEED-BEARING PLANTS) 522

XVI. EVOLUTION AND HEREDITY 571

TEXT-BOOK OF GENERAL BOTANY

PART I

CHAPTER I

INTRODUCTION

The Sciences.—Botany is one of the great divisions of knowledge which we call **the sciences.** Botany and the various other sciences, taken collectively, are spoken of as **science.** Science has been unsatisfactorily defined as **classified knowledge** but science means much more than a mere orderly arrangement of facts. Science includes properly only such facts as can be conveyed to the minds of others by definite and precise statement. It does not include any facts which have not been critically examined as to their truth and subjected to the test of experimentation or accurate observation.

Through classification and comparison of such facts, there are often brought to light certain broad and general truths which enable us to embody in one statement a great many known facts and to predict, with great certainty and without repetition of observations or measurements, a great many other facts. The discovery of these general truths, or **natural laws,** as they are called, is one of the chief ends of scientific study. In the search for such laws science makes use of certain tentative explanations, or **hypotheses,** which are products of the imagination of the scientific worker and correspond with all the facts which are known about the subject to which they are related. An hypothesis is not recognized, however, as a statement of a natural law until it has long stood the test to which it is constantly being put by the discovery of new facts. Many hypotheses which have finally been abandoned because of their failure to meet this test have, nevertheless, by reason of the stimulus which they have given to experimentation and to thought, greatly contributed toward the advancement of science.

Observation, description, comparison, classification, experimentation, inference—these are the methods of science. Feeling, that is to say, sentiment and emotion, must not be allowed to influence the scientist's decisions as to what is true and what is false. Although there is no valid reason why any field of human knowledge or experience should be closed against scientific inquiry, yet many of the most important facts of human experience, having to do with emotion, sentiment and faith, are by no means purely intellectual in their nature, and their worth is not necessarily to be judged by the purely intellectual standards of science. To insist that their value be judged by such standards is no more justifiable than to permit emotion and sentiment to enter into scientific thinking.

In this age in which we are able to converse with each other half way around the world, to travel hundreds of miles an hour through the air, to make machines perform most of our former drudgeries, and to avert, by the application of scientific knowledge, many of man's most dread diseases, it is quite unnecessary to emphasize the importance of science.

The constantly increasing store of truth which it furnishes and its great practical utility in our modern life are recognized by all. Nor are its benefits entirely material. From the pursuit of scientific truth many persons secure satisfaction of a very keen and elevating sort; and a knowledge of the laws of the universe which surrounds us has led many to a finer appreciation of the order and beauty of Nature.

Classification of the Sciences.—Most of the sciences have to do with material things, the substances of which they are made, their form and structure, and the changes which they may undergo. These sciences are sometimes spoken of as the **concrete sciences,** to distinguish them from mathematics and certain other sciences which are called the **abstract sciences** and which are not concerned primarily with objects. The concrete sciences may be divided into those which are concerned chiefly with non-living things (the **physical sciences**) and those which are concerned with living things or **organisms** (the **biological sciences**). To the group of the physical sciences belong chemistry, physics, geology, astronomy and many others.

Botany and Zoology—Distinctions between Plants and Animals.—Strictly speaking, **botany,** the science of plants, and **zoology,** the science of animals, together include all our knowledge concerning living things. However, certain branches of the study of animals, such as human anatomy, physiology and psychology, and certain divisions of the study of plants, such as bacteriology and plant pathology, are commonly spoken of as if they were independent sciences because of their great importance in relation to human affairs. To define botany as

the science of plants and zoology as the science of animals seems at first thought to distinguish clearly between the two biological sciences. On looking a little further into the matter, however, we find that the distinction is not so clear as it seemed, for it is by no means easy to define the familiar words, plants and animals. Indeed, it is impossible to draw a sharp line of distinction which will separate all plants from all animals, but the following points of difference apply to most plants and animals:

PLANTS	ANIMALS
1. The great majority of plants are not able to move from place to place. Many simple plants, are, however, capable of such movement (locomotion).	1. Locomotion (movement from place to place) is characteristic of most animals, although many animals, such as the sponges and the sea anemones, grow attached throughout most of their life.
2. In most plants each of the cells, or minute masses of living substances of which the bodies of all organisms are made up, is surrounded by a relatively rigid wall.	2. The cells of animals are generally without such surrounding walls.
3. Most plants have the power of building up from very simple substances, secured from the soil and from the atmosphere, the complex substances called foods which are used by all plants and animals to increase and replace living substance and for other life processes. Plants, therefore, could exist in a world devoid of animals.	3. Animals are unable to make their own foods. They must secure them from plants, either directly or through other animals. In a world devoid of plants, animals could not long continue to live. This, which is the most important distinction between typical plants and typical animals, does not, however, distinguish all plants from all animals, for there are several large groups of simple plants which are unable to make foods.
4. The growth in length of most plants takes place at or near the ends of the organs, and such growth generally continues as long as the plant is alive.	4. In animals, on the other hand, growth in length is seldom restricted to the extremities and generally ceases long before death occurs.

Among the larger and more complex organisms there is little difficulty in distinguishing which are plants and which are animals, but among the simplest organisms it is often very difficult and sometimes apparently quite impossible to maintain any distinctions between them. The reason for this is suggested by the **theory of evolution** which is the now generally accepted explanation of the origin of the hundreds of thousands of different kinds of organisms which now exist. According to this explanation all these kinds or **species** have developed by relatively slow changes from one or a few kinds of living things originally existing. It seems very certain that the original species, one or more,

were all plant-like at least in their power to manufacture food from simple substances secured from the soil, or water, and from the air. The first somewhat animal-like organisms which evolved from these original plant-like organisms were very much like the latter. Probably the differences could only have been distinguished by very careful study of their behavior. The simplest living things which exist to-day are doubtless very like those early forms and it is accordingly no easy matter to distinguish among them the plants from the animals. They include organisms which are considered by some to be plants and by others to be animals. Because of this, these organisms have come to be studied by both botanists and zoologists. As evolution went on, and more and more complex and larger organisms evolved, the distinctions became more and more marked.

The **protoplasm,** or living matter of plants and animals is essentially similar and, for the most part, the principles which govern the structure, development, and activities of plants and animals are fundamentally the same. Botany and zoology are, therefore, not unrelated sciences but have much common ground and are to a large degree interdependent.

Similarly, every science overlaps and shares part of the field of other sciences. Thus, **biology,** which includes botany and zoology, meets physics in the field of bio-physics, chemistry in the field of bio-chemistry, and geology in the field of paleontology, which is the study of the fossil remains of plants and animals. In such cases each of the sciences concerned may contribute new facts to the other. Thus the information which the botanist is able to supply as to the structure and relationship of the plants whose fossil remains are found in the rocks may assist the geologist in judging the age and origin of those rocks. The botanist, on the other hand, is indebted to the geologist for help in locating fossils of extinct plants and in gaining knowledge of the ancestors of present-day plants.

Pure and Applied Science.—Science is often divided into **pure science** and **applied science.** By pure science is meant scientific knowledge pursued without regard to its practical application to agriculture, industry, medicine, or other material interests. The worker in the field of pure science believes that the search for new facts and new laws is worth while for itself. The worker in the field of applied science prefers to direct his effort toward the securing of scientific material which will in some way contribute to improve the quantity or quality of some crop, to better the breeds of domestic animals, to introduce better methods in hygiene or medicine, to make more economical some manufacturing process, or to otherwise add to man's material well-being. Science had its beginnings, it is true, in the observations and specula-

tions of the ancients relative to things which were of immediate and practical interest to them. But it cannot be denied that the facts and principles upon which modern medicine, scientific agriculture, and many of the present-day wonders of electricity and mechanics are founded were revealed by men who sought to learn new things without in the least concerning themselves about the practical importance of what they learned.

Subdivisions of Botany.—Pure botany is commonly divided into **systematic botany, plant morphology,** and **plant physiology.**

Systematic botany, or **taxonomy** of plants, is concerned with distinguishing the different kinds of plants, describing each kind accurately, giving to each a name, and seeking to classify the different kinds so that those which are most closely related will be within the same group.

Plant morphology, which is concerned with the structure of plants, is generally subdivided into **external morphology** and **histology.** The first of these subdivisions has to do with the form and arrangement of the organs of the plant and with their structure in so far as these things can be studied without cutting into the plant body. Histology, which is the study of the internal structure of the plant, includes **anatomy** and **cytology.** Plant anatomy deals with the framework formed by the walls of the cells, while cytology is concerned with the structure of the minute masses of living material (protoplasm) by which the walls are built up and which are responsible for the growth of the plant and for all other life processes.

Plant physiology is the study of the activities of the plant, its growth, its methods of getting the materials from which it makes foods, the building up of these foods, the processes by which it produces other plants like itself, and all the other functions of the living plant. The plant physiologist seeks not only to describe, measure, and analyze these processes but to reduce them to the terms of physics and chemistry. In **plant ecology,** which is a branch of plant physiology, particular attention is given to the relations of plants to their environment in nature, that is to the soil, to temperature, to moisture supply, to light, and to the influences of the other plants and the animals which are associated with them. Plant ecology seeks to determine, among other things, why certain plants are restricted to particular locations and why they are generally found growing with certain other plants and with certain animals. There are many other special fields of pure botany which it is impossible to discuss here on account of limitation of space.

Applied botany, or economic botany, includes forestry, plant breeding, plant pathology (the study of the diseases of plants), horticulture, agronomy, and in fact all those branches of scientific agriculture which

have to do with plants. The Government of the United States, through the Bureau of Plant Industry and other agencies, and the different states, through their experiment stations, provide for the investigation of a large number of problems in applied botany and for the dissemination of the results of these investigations among farmers and others.

Physical and Chemical Principles Fundamental to the Biological Sciences.—It is impossible to study plants understandingly without a background of fundamental physical and chemical facts and principles. Particularly is this essential in considering the activities of the plant and its constituent cells, that is, in the study of plant physiology. It can not be expected that all of those who use this book, will have received instruction in physics and chemistry. For the sake of those students who have not had such instruction and by way of review for those who have, there will be introduced in this book from time to time, as suggested by the botanical context, brief discussions of the physical and chemical conceptions essential to a proper understanding of what follows. To set off these parts of the text from the purely botanical portions finer print will be used. The parts in fine print, however, are not to be considered of less importance than the rest of the book. They are absolutely essential to a proper understanding of the rest.

By way of introduction to these scattered notes are the following statements of fundamentals.

Through his senses man is aware of the existence of the universe about him. He sees, hears, feels, tastes and smells it. If sight, hearing, sense of touch, taste and smell were lost he might through his memory still be aware that various features of the universe had existed about him but would have no way of learning whether any particular feature still existed. The universe is then to man but the sum total of all the features which may affect one or more of his senses. All these features generally are spoken of in terms either of *matter* or of *energy*. Although recent advances in physics indicate that energy is the stuff out of which matter is made, still the distinction between matter and energy is a useful one.

Definitions, Their Use and Abuse.—It is necessary that these terms, matter and energy, be defined here but before that is done a note of warning must be sounded relative to the use of definitions. Definitions are essential if a writer or speaker is to express himself exactly and to be clearly understood by the reader or hearer. These definitions should be worded so as to express the meaning of the term in question as completely and precisely as possible. The student is, however, likely to fall into two very serious errors in the use of definitions. First, he is likely to take definitions too seriously and be satisfied with mere definitions and, second, he is likely to commit definitions to memory and be satisfied with mere words without regard to their real meaning.

A concise statement, such as a definition, can seldom make clear the full extent and the precise limitations of the meaning of a term. On that account the student should make his definitions as nearly perfect as possible and at the same time never be satisfied without knowing more than mere definitions.

It is the ideas involved, not the words, which are the essential things about a definition, and when a student learns the words by rote he is simply degrading his mind to the level of a mere automatic machine like the phonograph or the telephone receiver. Any tendency to do this may be avoided by trying, each time a given term is defined, to state the definition in different words.

Matter and Energy.—Matter is whatever has weight or occupies space. Energy is the capacity to do work or whatever can cause matter to move or change its rate or direction of motion. Different kinds of matter are called *materials*. Sandstone, oxygen, salt, cane sugar and water are materials. We distinguish different materials from each other by the way they affect our senses, that is to say by their different *properties*. Thus we recognize as sugar a white, sweet tasting material which disappears (dissolves) when placed in water. Man has learned to apply other tests besides the direct evidence of the senses to identify materials. Thus the chemist might make doubly sure that the sweet, white, soluble material was sugar by determining at what temperature it melts (melting point).

Light, heat, mechanical energy, and electricity are different forms of energy. Any one form of energy may be transformed into any other and such transformations are constantly going on within our own bodies and all around us, but these changes from one form to another are never attended by any loss or gain in the quantity of energy—none is ever made or destroyed.

Materials and Objects.—In considering matter it is important to distinguish clearly between a material (or substance) and an object (or body). An object is a certain quantity of material having a characteristic form. Thus a quantity of (the material) water, having a rounded (generally spherical) form, is a water drop and a water drop is an object. Similarly a round mass of air, visible of course only when surrounded by a liquid or a solid, is a bubble. Air is a material, a bubble is an object. The material (kind of matter) of which an object consists is generally secondary in importance to its form and dimensions. Thus, cups may be of iron, silver, wood, glass or clay; and from a single material, iron, for instance, nails, rails, knives, hooks, beams, screws and a great variety of other objects may be made.

States of Matter.—All the materials with which we are familiar are solids, liquids or gases. By a solid we mean material in such a state that a continuous mass of it can not flow or be poured. A solid does not take on the form of any vessel in which it is placed. A liquid, on the other hand, can be poured and always accommodates itself, in as far as it fills it, to the form of any empty vessel in which it is placed. A gas is invisible unless it has a characteristic color. Furthermore, it not only takes on the shape of any empty vessel (one containing not even gas) in which it is placed but will expand to completely fill the vessel no matter how little the quantity of the gas. Solid, liquid and gas are not different materials but merely different states, for the same material may exist in the three different states as in the case of ice, water and water vapor. The three states are characteristic of the material at low, intermediate and high temperatures. Thus butter at the temperature of a warm summer day becomes a liquid, kerosene heated to a high temperature becomes a gas and oxygen reduced to a very low temperature becomes a liquid. A very remarkable fact having to do with the change from one state to another, is that a considerable quantity of heat is liberated when a gas becomes a liquid or a liquid changes to a solid. When the transformations are in the opposite order corresponding quantities of heat are absorbed.

Density.—Every object has a certain weight. Its weight is an expression of the degree to which it is attracted by the earth (attraction of gravity). We determine

its weight by comparing its attraction by the earth with the earth's attraction for one or more standard objects (one or more of a set of weights) arbitrarily chosen. Weight is a property of an object or given *quantity* of matter, not of a given *kind* of matter. We do not say iron weighs 8 grams and gold 19 grams. That is meaningless. We say rather that a cube of iron 1 centimeter on each edge weighs about 8 grams or that a cubic centimeter of gold weighs about 19 grams.

Matter does have a property, called *density*, which is characteristic of *kinds* of matter, not *quantities* of matter, and is yet closely related to weight. Density means the relative weights of equal volumes of different materials. This is the property which we have in mind when we say that lead is a heavy metal and aluminum a light metal or that cork is lighter than water. Density may also be defined as the different degree to which equal volumes of different materials are attracted by the earth. By general agreement densities of solids and liquids are expressed in terms of weight in grams per cubic centimeter. We have then only to weigh a cubic centimeter of a solid or liquid material to determine its density. Since given weights of matter almost always occupy a greater volume at higher temperatures and a lesser volume at lower temperatures, that is to say expand and contract as the temperature rises and falls, the density of a material varies with temperature. In the following table of some common materials the densities, except where otherwise specified, were determined at 18° Centigrade.

Aluminum	2.7	Lead	11.3
Cane sugar	1.59	Platinum	21.4
Common salt	2.16	Glycerine	1.26
Cork	0.2	Petroleum	.8
Gold	19.2	Quicksilver	13.55
Iron	7.8	Water	.998 (at 4° the density of water is 1. That is its greatest density.)

Gases also differ in density. Hydrogen has a lower density than any other gas.

Elements and Compounds.—In the case of most materials, such as water, salt, cane sugar, etc., it is possible to decompose the substance into two or more different simpler substances. For instance, by the passage of an electric current through it, water may be decomposed into the two gases, oxygen and hydrogen. All attempts to break down oxygen and hydrogen into simpler substances have failed.[1] Similarly cane sugar can be decomposed or broken up into oxygen, hydrogen and carbon, but carbon also has resisted all attempts to break it down into simpler component substances.

Although they have analyzed thousands of different kinds of materials, chemists have found only about ninety of these simple elementary substances or *elements*. A few of the best known or most widely distributed of the elements are oxygen, nitrogen, hydrogen, carbon, sulphur, phosphorus, potassium, sodium, chlorine, cal-

[1] There are, however, several elements (the radioactive ones) which break down spontaneously into other elements. Thus radium yields helium and lead. It has thus far proven impossible for man to cause such disintegration or to slow up or hasten the process in any way. Thus it is literally true that the elements have resisted all attempts to break them down into simpler substances. Furthermore, there is in the case of most of the elements no evidence of any spontaneous disintegration into other elements.

cium, magnesium, iron, aluminum, gold, silver, tin, platinum, and copper. Any of the elements can exist in a pure condition, uncombined with other elements.

All materials except such uncombined elements are either *compounds* or *mixtures* of two or more compounds or elements. A compound always consists of two or more elements united in certain definite and constant proportions. Such materials as water, cane sugar and common salt are examples of compounds. Water, as we have already learned, is composed of the elements hydrogen and oxygen. When any quantity of water is decomposed the proportions of the two elements are always the same, two parts by weight of hydrogen to sixteen of oxygen. Similarly common salt is composed of sodium and chlorine in the proportions by weight of 23 to 35.5. It is this unvarying proportion between the quantities of the different elements which distinguishes a compound from a mixture, for in the latter case the ingredients may exist in all conceivable proportions.

Atoms and Molecules.—If it were possible to divide a piece of some compound into smaller and smaller pieces, we would find sooner or later that we had particles so fine that further division was impossible without separating them into simpler compounds or into the component elements. Such particles, the smallest particles of any particular compound, are called molecules.

All the molecules of a given compound have the same weight. If we attempted to divide a molecule of water we would get oxygen and hydrogen instead of water. Molecules of a compound are composed of one or more units of each element present. These unit particles of any element are all of the same weight or very nearly the same weight.

The following statements will serve to illustrate the relation of the terms just explained. A piece of cane sugar consists of a great many sugar molecules all of the same weight. Each such molecule is made up of twelve carbon atoms, twenty-two hydrogen atoms and eleven oxygen atoms. A single atom of carbon weighs almost exactly twelve times as much as an hydrogen atom.

Several atoms of a single element can combine to form a molecule of that element. Thus oxygen gas under ordinary conditions is made up of oxygen molecules, each consisting of two oxygen atoms and similarly the molecules of hydrogen consist of two atoms each.

Pure Substances.—A material made up of only one kind of molecules or of only one kind of atoms is called a *pure substance.* If only one kind of atom is present in a pure substance the substance is an element. If more than one kind of atom is present it is a compound.

Transformation of One Form of Energy into Other Forms.—Mention has already been made of the fact that there are a number of forms or varieties of energy and that energy can be transformed from one form into others but without any gain or loss in the total amount of energy involved. These facts can be made somewhat clearer by means of illustrations taken from everyday life. The mechanical energy of a waterfall directed against a water wheel or turbine which rotates a dynamo is transformed into electrical energy. In our homes this electrical energy is transformed by the toaster or electric stove into heat energy, by the electric light bulb into light energy and by the motor into mechanical energy again. The decomposition of water by an electric current into oxygen and hydrogen, of which we have already spoken in another connection, involves a transformation of electrical into chemical energy which may be said to be stored in the oxygen gas and the hydrogen gas. The hydrogen and oxygen if mixed and lighted will burn and the chemical energy will be transformed into heat energy and light energy. If the mixture of gases were ignited in

the cylinders of an automobile, part of the energy would be in the form of mechanical energy just as when gasoline vapor and oxygen explode in the operation of an automobile. Such transformations are of great importance, for the activities of plants and animals, including man, and all the operations of industry consist largely of such transformations.

Classification of Plants.—There exist to-day upon the earth over a quarter of a million different kinds of plants. A great many kinds which flourished in the past are now extinct. Among the many kinds now existing there are clearly certain ones, such as the different oaks, which resemble each other more closely than they do any other plants. From very early times, certain of these clearly marked groups of plants have been recognized and men have tried to classify such small groups of plants and animals in various ways.

The first serious attempt at the classification of plants of which we have record was made by Theophrastus, a Greek philosopher and pioneer in the field of science. He lived between 370 and 285 B.C. and was a student of both Plato and Aristotle. In his principal botanical work, "The Enquiry into Plants," Theophrastus shows such a keen perception of the essential differences between different kinds of plants, and such a genius for their classification that he has been very properly called the first systematic botanist. His works include descriptions not only of the plants of Greece and adjoining countries but also of plants found only in countries much farther east. His knowledge of these plants he owed largely to Alexander the Great, who took with him, on his expeditions into the East, trained men who could make accurate observations of the plants they saw.

[2] No very important advance over the work of Theophrastus was accomplished by other classical botanists or by those of the Middle Ages, although Dioscorides about A.D. 80, described some four hundred medicinal plants in his "Materia Medica," which was in general use even up to the seventeenth century. From about 1600 to the middle of the last century, great advance was made in the field of plant classification, the most important representative of the period being the Swedish botanist, Linnæus. Since his time there have been put forward several systems of classification, each representing a distinct advance over the preceding. The most important of these were that of Bernard and Antoine Laurent de Jussieu, that of A. P. de Candolle and his fellow-workers, embodied in the "Prodromus Systematis Regni Vegetabilis," that of Bentham and Hooker, published in their "Genera Plantarum," and the system put forward by Engler and Prantl in their

[2] Some of the material of this and the previous paragraph is drawn from Jepson's "Economic Plants of California."

" Natürlichen Pflanzenfamilien " (The Natural Plant Families). Limitation of space prevents even the mention of a number of men who made very significant contributions to this field.

All systems of classification of plants are either **artificial** or **natural classifications,** or a combination of both. An artificial classification is one in which there is no recognition of any actual relationship between different kinds of plants, in the sense of common descent. An artificial classification may be based upon such superficial characteristics as flower color or leaf form, although plants with the same flower color or leaf form, may be much less closely related to each other than they are to certain plants having very different colored flowers, leaves of entirely different form, or both. All the earlier classifications were very largely artificial, for those who made them believed that each kind of plant or animal had been specially and separately created (the Theory of Special Creation) and that once created, no kind of organism could ever give rise to any other kind (the Theory of Constancy of Species).

As long as those beliefs were held it was inconceivable that there could be any relationship, in the sense of common descent, between different species, no matter how many points of resemblance there might be between them. With the acceptance of the doctrine of evolution, botanists came to look upon all plants as being related and attempted to so classify them that each group included kinds of plants more closely related to each other than to any other kinds, that is, plants having a great part of their ancestry in common. Such a classification is called a natural classification.

Because of the incompleteness of our knowledge of the relationships of plants and for other reasons, it is not possible for us to so classify plants as to show all their relationships. Accordingly, our present-day classifications are partly artificial and partly natural. The principal goal of the systematic botanist is, however, to work out a classification of plants which will correspond as closely as possible with their actual evolution.

Plant Characters Used as a Basis of Classification.—In all higher plants there are reproductive organs, such as flowers and fruits, and vegetative organs, such as roots, stems and leaves. Reproductive organs are less influenced by environmental conditions than are vegetative organs. There may be little resemblance between the vegetative portions of two species, although their reproductive structures may be very similar. For example, the strawberry and the raspberry although closely related, have quite different growth forms, that is, their vegetative organs are quite dissimilar. However, the flowers of

the two are constructed on the same general plan. On the other hand, two plants with very dissimilar reproductive structures may resemble each other very closely in their general vegetative appearance, especially when they grow under the same external conditions. Although vegetative structures may be modified to a great degree under diverse environmental influences, these same influences do not modify, to an equal extent, the reproductive organs. On account of this greater stability of the reproductive structures, they are of relatively greater value than the vegetative structures in showing actual relationships, and are of prime importance in classification.

The Groups Making up the Plant Kingdom.—There are on the earth an immense number of individual plants. A careful examination of any two plants will show that, even though they may be very much alike, there are individual differences between them. Every one of these individuals is the offspring of one or, in most plants, of two parents. Every individual is a point in one of the many long lines of descent leading back into remote time. If we could trace these lines back we would find that at each generation they merged with other lines, just as we find in tracing the genealogies of human individuals. According to the theory of evolution, if we could follow these lines of descent back far enough we would find that all the individuals had descended from one or a few very simple organisms. This means that perhaps all plant individuals are related or at least that within each of a few great groups of plants all individuals past and present have descended from the same remote ancestors.

Species.—Everyone recognizes that among the myriads of individual plants about us there are different kinds such as the oaks, the roses or the pines. If the oaks are studied with some care it is found that there are many recognizable kinds of oaks and so it is with the roses, the pines and other plants. Now it has been generally agreed to speak of each recognizable kind as a **species** (plural also **species**). Each species consists of a group of individuals which are very much alike. Most of the differences between the individuals of a species are not inherited but are due to the effect of external conditions. Any two individuals of a species are assumed to be more closely related, that is, more recently descended from the same ancestor, than are two individuals of different species.

The differences between two closely related species are supposed to have originated through new characteristics which arose among the individual progeny of their common ancestors and which were inherited.

Genera and Larger Groups.—Species which are similar in many respects and which are presumably more closely related to each other

than to other species constitute a **genus**. Similarly genera (plural of genus) are grouped into larger groups and these into still larger groups as shown in the following arrangement. (Adapted from Bessey and Bessey.)

Species consist of individual plants
Genera are composed of species
Families are collections of genera
Orders are collections of families
Classes are collections of orders
Divisions are collections of classes
The Vegetable Kingdom is a collection of divisions.

Accordingly

Every plant belongs to some species
Every species to some genus
Every genus to some family
Every family to some order
Every order to some class
Every class to some division
All divisions to the Vegetable Kingdom.

It is important to bear in mind that individual organisms, plants and animals, are the only things in the plant or animal kingdom which actually exist. A species is merely a mental conception of a group of individuals sufficiently alike and closely enough related to be considered as one kind. A genus is a conception of a group of similar and related species, etc. Such groupings of plants or animals are nevertheless of great practical and theoretical importance in botany and zoology.

For many years it has been common practice to divide the whole Plant Kingdom into four divisions:

1. THALLOPHYTA, which includes a great variety of simple plants such as the pond scums, bacteria, molds and mushrooms together with some larger and more complex plants such as the seaweeds.
2. BRYOPHYTA, or mosses and related plants.
3. PTERIDOPHYTA, or ferns and related plants.
4. SPERMATOPHYTA, or seed-bearing plants.

The first of these groups includes such a variety of different kinds of plants, many of which have very little in common, that there is a growing feeling that they should not all be included in a single division. Until systematic botanists have come nearer to an agreement upon the great groups of plants the old classification will continue to be widely used.

The method of classifying plants is illustrated below by the complete classification of a common garden rose and of wheat.

Division	Spermatophyta	Spermatophyta
Class	Angiospermae	Angiospermae
Sub-class	Dicotyledonae	Monocotyledonae
Order	Rosales	Graminales
Family	Rosaceae	Gramineae
Genus	Rosa	Triticum
Species	cinnamonea	vulgare
	Cinnamon Rose (*Rosa cinnamonea*)	Common Wheat (*Triticum vulgare*)

Naming of Plants.—The name of the genus to which a plant belongs taken together with the name of the species of the plant are spoken of as a **binomial.** This combination of generic and specific names is used as the scientific name of the kind of plant in question. The generic name has the form of a Latin noun, while the species name is an adjective. This method of naming plants or animals is called **"binomial nomenclature."** Among the first to employ it was the great Swedish naturalist, Linnæus through whom it came into general use among botanists and zoologists. He was born in 1707 and was the son of a village pastor. In spite of great poverty and other obstacles he persisted in his efforts to secure a medical degree and to acquaint himself with natural history. He became a practicing physician in Stockholm but devoted his time largely to botanical studies, the results of which soon made him famous throughout Europe. In 1741 Linnæus became Professor of Natural History at the University of Upsala, where he had the most favorable opportunities to continue his systematic

FIG. 1.—Linnæus (Carl von Linné) (1707–1778), the father of modern taxonomy. (From Gager).

studies of plants, animals, and minerals. He was an excellent teacher and attracted many students to Upsala.

Linnæus named a great number of our now commonly known plants and animals, as well as many rarer ones. Since it is the accepted practice to place after a binomial an abbreviation of the name of the man who first used that combination of genus and species name, we find the initial letter of Linnæus' name attached to many scientific names. Some of these Linnean species of plants are *Beta vulgaris* L. (common beet), *Brassica rapa* L. (turnip), *Pyrus malus* L. (apple), *Pyrus communis* L. (pear), *Pisum sativum* L. (garden pea), *Trifolium pratense* L. (red clover), *Medicago sativa* L. (alfalfa), *Daucus carota* L. (carrot), *Solanum tuberosum* L. (potato), *Avena sativa* L. (cultivated oat) and hundreds of others.

Origin and Meaning of Scientific Names of Plants.—The specific name is often descriptive of some feature of the plant which was thought by the person who originally described and named it to be characteristic. Examples of such descriptive specific names are *sativus*, meaning edible; *communis* and *vulgaris* meaning common; and *alba* and *nigra*, meaning respectively, white and black. The last two specific names are very frequently used. For example, in the genus *Brassica* both of these specific names are employed, *Brassica alba* being white mustard and *Brassica nigra* being black mustard. Not infrequently a specific name is formed from the name of the person who first collected the plant in question or of some person whom the botanist naming the plant wished to honor. For example, a western sand cherry is named *Prunus besseyi*, the specific name being formed from that of the botanist, Bessey. Generic names are often merely the words by which the plants in question were known to those who spoke the Latin language. Examples of such names are *Avena* (oat), *Pinus* (pine), *Quercus* (oak), *Phaseolus* (certain kinds of beans), *Pisum* (pea), and *Ficus* (fig). In other cases the names of genera are descriptive, as in *Trifolium* (*tres*, three and *folium*, leaf), the name of certain clovers whose leaves are three parted; and *Saccharomyces* (*Saccharon*, sugar and *Myces*, fungus) a generic name used for the common yeast which are fungi (Thallophyta which are unable to make their own food) living largely upon sugars. Genera are also sometimes named after persons, for example, *Eschscholtzia* (California poppy) named after the botanist, Eschscholtz.

The names of plant families are usually based upon some outstanding characteristic of most of the genera of the family, as in the case of the *Leguminosae* which bear their seeds in a legume or pod; or upon the name of one of the principal genera of the family, as in the case of *Solanaceae* which are named after the genus *Solanum*.

Use of Common Names and Scientific Names.—Though it is often convenient to use the common names of plants instead of the scientific names, there are many reasons for employing the latter whenever we wish to avoid all uncertainty as to the particular plant to which we refer. Many common names are strictly local in their use and in other regions are either not used at all or are applied to some other plant. Several distinctly different plant species, which may or may not be related, are often included together under one common name.

The settlers in the North Coast ranges of California apply the name Post Oak to *Quercus garryana;* the ranchmen in certain parts of the Sierra foothills ascribe the name Post Oak to *Quercus douglasii;* and in the eastern states the same common name is given to an entirely different species, *Quercus stellata.* In other cases, a great number of common names are used for a single species. For example, *Pinus ponderosa* is given such common names as "Bull Pine," "Black Pine," "Yellow Pine," and many others. It is scarcely to be expected that a Russian, French or Japanese common name will be accepted and generally used by persons who speak other mother tongues than these. It is therefore best to employ for scientific purposes the universally accepted binomials which, being in the Latin form, belong to a language which is not spoken by any living people but is probably more familiar to educated people in general than any living language. The use of **one** scientific name does away with much misunderstanding as to what the plant is, to which reference is made.

CHAPTER II

THE PLANT BODY

The Individual Plant.—The Plant Kingdom is made up of a great number and variety of individual plants. Each individual plant, whether it be a single wheat plant among millions in a field, or a single bacterium among countless others in the soil, or a single tree among its many neighbors in a forest is a distinct and individual organism which is able to carry on all the life processes necessary to maintain its life and perpetuate the species. It has a parent or parents, and a long line of ancestors behind it.

The individual plant must carry on the different processes necessary to maintain its life, must often undergo unfavorable environmental conditions such as extremes of temperature, must compete with its neighbor plants for space in which to grow, must often be subjected to the attacks of insects or other parasites, and finally, must produce offspring.

The activities of the individual plant are two-fold: **vegetative activities** and **reproductive activities.** The principal vegetative activities, that is, **those which have to do with the growth and preservation of the individual,** are **absorption** of raw materials from the soil, **transfer** of the raw materials in the plant body, **manufacture of food, assimilation** (the process by which foods are transformed into the living material—protoplasm), **respiration,** (a " breaking down " of substances in the cell, which provides energy for the work of the plant and in which oxygen is taken in and carbon dioxide given off), and **transpiration,** (water loss). Reproductive activities are **those which have to do with the preservation of the species of plants to which the individual belongs.**

Organs and Tissues.—We speak of the human body as being made up of a number of organs, each with a work to do. There are organs of sight, of hearing, of digestion, etc. Just so, we may speak of the **plant body.** It, too, is composed of various organs, with which it carries on its different activities. An **organ** is a part or member of the plant with a particular kind of work to do. For example, the roots are absorbing and anchoring organs, the stems are conducting and supporting organs, the leaves are food-making and transpiring organs,

and the flowers are reproductive organs. If we study microscopically the structure of organs, we find them to be made up of many small sacs with walls which are usually thin and transparent. Each of these small, microscopic sacs or compartments is called a **cell.** Just as a brick house is made up of separate units, the bricks, so is the plant body made of separate units, the cells. It is in the cells that all the complex physical and chemical changes of the living body go on. Cells of similar structure which together perform a special function constitute **a tissue.** Thus the leaf is composed of several different kinds of tissues such as conductive tissue, protective tissues, and food-making tissues.

Some plants have but few distinct organs, or a few tissues, with which to carry on the different functions. Such plants are said to be simply organized. Among such simply organized plants are the bacteria, the pond scums, seaweeds, molds, mildews, rusts, smuts, etc.

Many plants have numerous distinct organs, and many tissues which carry on the separate functions. This is true of the commoner plants of orchard, garden, field and forest. Such plants are said to be highly organized.

Different Kinds of Plant Bodies.—In the simplest plants the plant body consists of a single cell. Within this simple plant body are carried on all the life activities. Examples of such one-celled organisms are bacteria, *Protococcus* (Fig. 236) which constitutes the green growth commonly found (in the northern hemisphere) on the north side of tree trunks, fence posts and walls and *Sphaerella nivalis* ("red snow"). The plant body of such organisms is surrounded on all sides by water and a supply of materials from which food can be absorbed or built up. Such an organism has no need for special absorptive tissue or conductive tissue since all its functions are carried on within a single cell.

A plant body in which cells are joined end to end to form a thread or filament represents an advance in complexity over the unicellular forms. There are numerous filamentous or thread-like algae, such as *Spirogyra* (Fig. 239) (one of the pond scums), and *Oedogonium* (Fig. 246); and also many filamentous fungi, such as certain molds, mildews, rusts and smuts. In *Oedogonium*, a basal cell of the filament may become differentiated as a **holdfast cell;** and certain other special cells of the filament may take on, in addition to nutritive functions, the reproductive function, whereas the majority of the cells have only nutritive functions. Here there is a slight degree of specialization.

In some of the seaweeds (*Ulva*, or sea lettuce) the plant body is flattened. It consists of a plate of cells, two cells thick. In other more complex seaweeds (Fig. 255) and in such fungi as mushrooms

(Fig. 306), there is a rather complex and extensive plant body. The molds, mildews, rusts, smuts, and fleshy fungi, such as the mushrooms, have various forms of plant bodies, some large and complex; but in none of them, nor in any of the algae, are there true stems and leaves.

The Plant Body of Seed Plants.—In the plant body of seed plants which include almost all our crop plants (Fig. 2), the stems, foliage leaves, and roots are chiefly concerned with maintaining the life of the individual, that is, carrying on the **vegetative** functions, such as absorption of materials from the soil, manufacture of foods, respiration, transpiration and assimilation, whereas the flowers, which produce seeds, carry on the **reproductive** activities, and thus assure the continuance of the race.

The plant body of the seed plant is made up of **shoot** and **root.** The shoot, which is made up of two kinds of organs, **stems** and **leaves,** generally grows upward into the air, whereas the root grows downward into the soil. The stem is divided into nodes and internodes, regions which alternate throughout the length of the stem. **Nodes** are slightly enlarged portions of the stem where leaves and buds arise, and where branches originate. An **internode** is the region between two successive nodes.

Principal Distinctions Between Stem and Root.—The stems and roots are both cylindrical structures which, in some cases, are distinguished only with difficulty. The following are the principal differences between stems and roots:

1. Normally, branch stems arise only at nodes, and in the axils of leaves; whereas roots branch irregularly, there being no division of roots into nodes and internodes.

2. The internal structure of the stem differs from that of the root.

3. Stem branches originate at the surface of a main stem and near its extreme tip; branch roots arise, not at the surface, but within a larger root and at some distance from its tip.

4. The growing point at the extreme tip of the stem is covered and protected by rudimentary foliage leaves and in some cases by modified leaves, the **bud scales.** The growing point of roots, however, is protected by a special thimble-shaped structure, the **root cap.**

Functions of Stem, Root, and Leaf.—The primary functions of the stem are (1) the support of foliage leaves and floral leaves (flower parts); (2) the **conduction of water** and **mineral salts** from the soil; and (3) the **conduction of plant foods** from the points where they are manufactured to points where they are needed in growth or where they will be stored for future use.

In addition to these primary functions of stems, there are certain

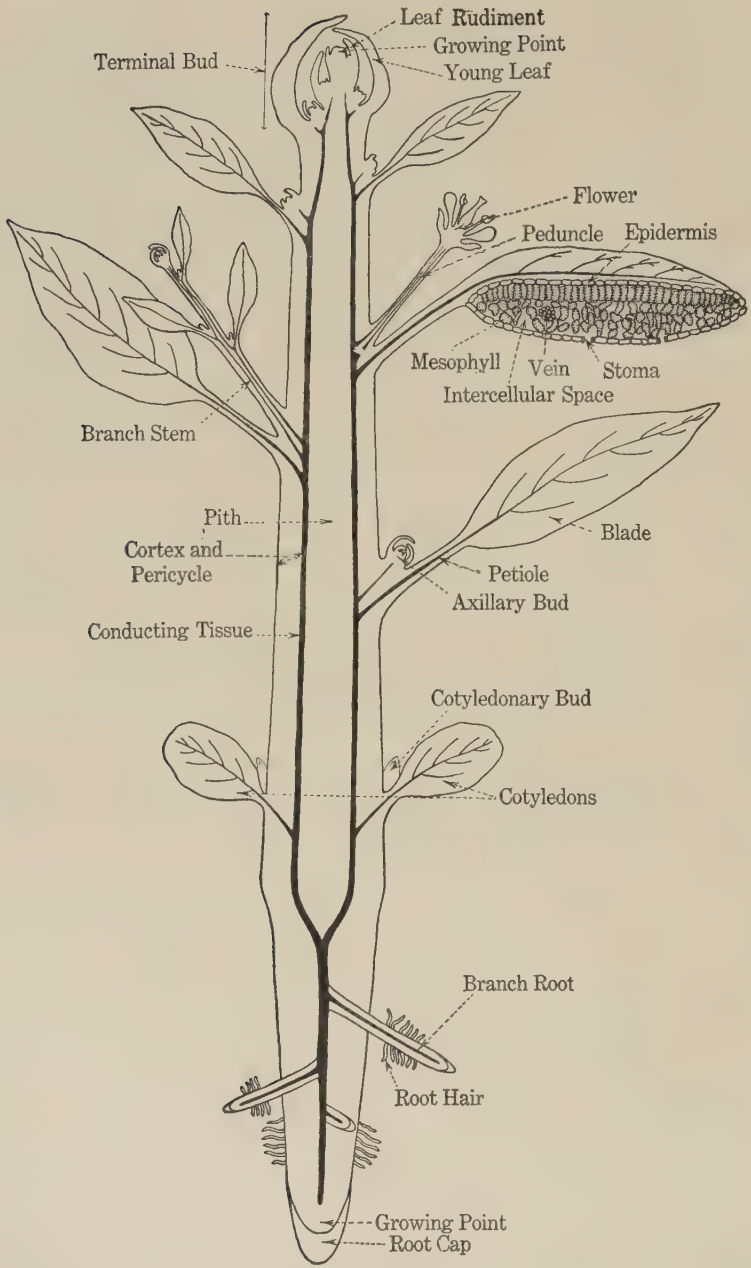


FIG. 2.—Diagram showing the principal organs and tissues of a typical seed plant. (Modified after Sachs.)

secondary ones. The stems of most non-woody plants and the youngest stems of woody plants are green and are able to supplement the leaves in food manufacture (photosynthesis).

Some stems act as storage organs. For example, in the underground, enlarged stem (**tuber**) of potato (Fig. 104), a large amount of starch is stored; also, in the twigs of the common orchard trees considerable quantities of reserve food are stored in the form of starch and sugar. The cacti and various other plants of desert regions have thick fleshy stems within which water is stored.

In some plants the stems act as organs of vegetative reproduction. For example, the underground stems (rootstocks or rhizomes) of such plants as quack grass (*Agropyron repens*) (Fig. 102), Canada thistle (*Carduus arvensis*), false Solomon's seal (*Smilacina*), and iris are capable of sending out aerial stems and roots from the nodes. When such underground stems are cut or broken into a number of pieces, each piece, if it includes one or more nodes, may send out new stems and new roots. Likewise, some aerial stems have this power. The runners (creeping stems) of the strawberry (*Fragaria*, Fig. 107), the tubers of the potato (*Solanum tuberosum*), the bulbs (short stems with fleshy leaves) of onion (*Allium cepa*, Fig. 105), the corms (fleshy stems, Fig. 106) of cyclamen are propagative organs and are used commercially as a means of multiplying the plants.

The primary functions of the root are (1) **anchorage,** and (2) **absorption** of (*a*) water and (*b*) certain mineral (inorganic) salts. A secondary function is food storage. Common examples of roots which act as storage organs are those of sugar beet (*Beta vulgaris*), radish (*Raphanus sativus*), turnip (*Brassica rapa*), parsnip (*Pastinaca sativa*), and sweet potato (*Ipomaea batatas*).

The primary functions of the leaf are the **manufacture of carbohydrates** (photosynthesis), the **synthesis of nitrogenous foods,** and **transpiration** (water outgo).

Balance Between Shoot and Root Systems.—In an earlier paragraph it was stated that the plant body consists of two main parts: (1) shoot, and (2) root. These two not only differ structurally, but they differ in the work they have to do. The shoot is chiefly concerned with the manufacture of food and the development of reproductive structures. The root is chiefly concerned with absorption and anchorage.

It is well recognized that, in transplanting plants and in pruning, a balance must be maintained between the root and the shoot. The root system must be extensive enough to supply the shoot with sufficient water and mineral nutrients. The shoot must be adequate to

manufacture sufficient food for the maintenance of the root system. For example, when a young orchard tree is transplanted, many of the roots of the young plant are necessarily destroyed; consequently the

FIG. 3.—Excurrent type of branching (pine). (Photograph by E. Fritz.)

absorbing surface is reduced. The approved practice is to cut back or thin out the shoot (remove branches here and there) and thus attempt to re-establish the balance between the two systems. The reduced root system will be unable to adequately supply the tissues of the shoot

with water and salts unless the latter is also reduced. On the other hand, a too severely pruned shoot does not permit of normal growth and development, for the few green leaves which it will bear will be insufficient to supply food for the relatively large root system, which is

FIG. 4.—Deliquescent type of branching (elm). (Photograph by E. Fritz.)

itself incapable of making food. A condition of unbalance between root and shoot, if not corrected, will retard the plant's development and may cause its death.

General External Features of the Shoot, Especially of Woody Plants.—Three general types of shoots are recognized: **Erect, prostrate** and **climbing.** The shoots of most plants grow **erect.** The shoot of

such plants as the cucumber, squash, watermelon and strawberry are **prostrate** on the ground. Plants which climb upon other plants and depend upon them for mechanical support, that is, plants with climbing shoots, are known as **lianas.** Examples of lianas are the scarlet runner bean (*Phaseolus*), dodder (*Cuscuta*), hop (*Humulus*), bitter sweet (*Solanum dulcamara*) and grape (*Vitis*).

There are two principal forms of erect shoots, **excurrent** and **deliquescent.** Pines, spruces and firs have an elongated or cone-shaped shoot system. In these there is a single main stem with many lateral branches. Also, in the Carolina poplar there is a "leader"—one main stem which throughout the life of the plant holds this leadership. This type of stem is said to be **excurrent.** In the oak, common cottonwood, apple, peach and many other angiosperm trees, the principal stem is replaced by the upper lateral branches, so that it is impossible to pick out any one main stem. In these, some lateral branches develop with as great vigor as does the original main stem. This type of shoot is called **deliquescent.**

Trees, Shrubs and Herbs.—The classification of plants into trees, shrubs and herbs is much used and very convenient, although there is no very sharp line of distinction between these three classes. Trees include those plants whose stems are largely made up of wood and which remain strong and erect when they undergo great water shortage or in fact even after they are dead. Plants whose stems develop very little wood but consist mostly of soft tissue and which become weak and droop or collapse (wilt) when they are unable to secure or retain sufficient water, are spoken of as **herbs.** The shoots of trees and shrubs generally persist for years while those of herbs (at least the parts above ground) generally die each year except in regions where there is no very cold or very dry season.

By trees we mean tall woody plants having generally a single main stem or trunk, at least for some distance above the ground. Shrubs on the other hand, are shorter woody plants more freely branched than trees and frequently having even at the base no single main stem. In practice the principal distinction is one of size.

Buds.—A bud consists of a short length of partially developed stem with rudimentary leaves in various stages of development. Some of these rudimentary leaves are large enough to enclose or enfold the extreme tip of the stem within the bud. Whereas the internodes of mature parts of the stem are generally considerably elongated, several inches long in some stems, the internodes of the partially developed part of the stem within a bud are very short.

That a bud is actually a partially developed stem is clear when we

cut it lengthwise and study its structure. It is also shown by the fact that branches always develop from buds. Buds may, in the case of many species of plants, be removed from the stems on which they originated and with certain precautions set into the stems of other plants where they will subsequently develop into branches. Such bud grafting is a common horticultural practice.

The delicate growing point (extreme tip of the stem within the bud) and the rudimentary leaves, especially in the case of most trees

FIG. 5.—Bud-grafting. From left to right; cutting T-shaped cleft in bark of stock; bud partly inserted in cleft; bud inserted and ready to be bound; bud bound tightly, bringing cambium of bud in contact with that of the stock. (From the Division of Pomology, College of Agriculture, of the University of California.)

and shrubs of cold and arid climates, are usually protected by several layers of overlapping scales (bud scales) which are modified leaves (scale leaves, Fig. 6). Bud scales may be covered with hairs, as in the willow, or with a waxy secretion, as in the cottonwood. These coverings very effectively protect the enclosed tender structures from rapid drying out as well as from mechanical injury. **Naked buds** are not protected by scales; they are found on woody plants of the moist tropics, and on herbaceous plants the world over.

Classification of Buds.—Buds may be classified (1) as to their position on the stem, (2) as to the number at a node, (3) as to the structures which they contain, and (4) as to their development.

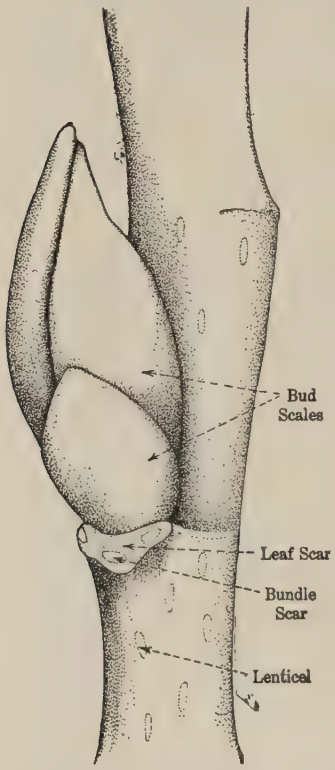


FIG. 6.—External view of a portion of a cottonwood stem showing an axillary leaf bud, leaf scar and lenticels.

As to their position on the stem they may be: (*a*) terminal, (*b*) axillary, and (*c*) adventitious.

Most branches end in a bud, which is called the **terminal bud** (Fig. 2). As a rule, the stem which develops in a single season from a terminal bud is longer than any of those which develop from other buds on the same branch.

Axillary buds are buds which regularly arise in leaf axils, that is, just above the place on the stem where a leaf is attached. They may give rise to leafy branches or to flowers. On very short branches (spurs) it is sometimes difficult to distinguish between terminal and axillary buds. **Accessory buds,** (Fig. 8) which are well illustrated in the maples and box elder (*Acer*), are extra ones in addition to the axillary bud proper, which come out in the leaf axils.

Adventitious buds are buds which arise anywhere on the plant except at the tip of the stem or in the leaf axils. They may arise on stems or roots, or even leaves. Their formation is usually stimulated by injury. For example, when a branch is cut back, as in pruning, numerous adventitious buds may arise at the edges of the cut surface.

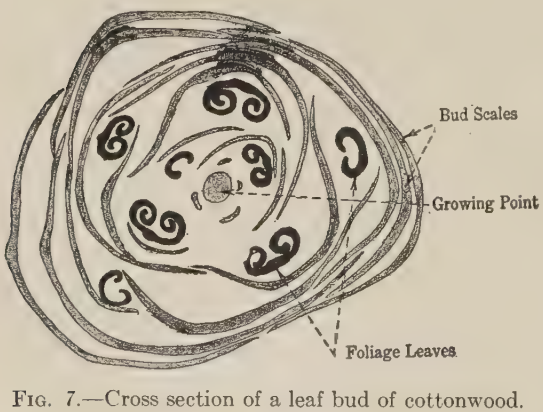


FIG. 7.—Cross section of a leaf bud of cottonwood.

Axillary buds may be classified **as to the number at a node into:** (*a*) alternate, (*b*) opposite, and (*c*) whorled. When one bud occurs at

each node, as in the apple, peach, plum, and cottonwood, they are said to be **alternate.** When two buds stand at a node and on opposite sides of the stem, as in the mints, box elder, and maples, they are **opposite.** When more than two buds stand at a node, as in catalpa, they are said to be **whorled.**

As the structures which they contain, buds may be (*a*) leaf, (*b*) flower or fruit, or (*c*) mixed buds. When a **leaf bud** is opened there is found a much shortened axis or stem bearing a number of small leaves. As indicated, a bud is a young stem; consequently a leaf bud may as properly be called a **branch bud**; since it may elongate into a branch stem bearing leaves. The new stem, just as the old one from which it came, has buds in the axils of its leaves and itself ends in a terminal bud.

FIG. 8.—A portion of a peach twig showing buds. In the peach, three buds occur at a node—a single leaf bud with a flower bud on each side. (After Tufts, in California Agr. Exp. Sta. Bulletin.)

A **flower** or **fruit bud** is one containing flower parts but no foliage leaves. If we open a bud of this type, we find one or more young, unexpanded flowers (Fig. 9). The number of flowers in the bud of a given individual plant is not constant. Fruit buds are rarely terminal, as in the loquat (*Eriobotrya japonica*) but are commonly lateral, as in stone fruits: peach, plum, apricot, cherry, almond (*Prunus*), in gooseberry (*Ribes*), and walnut (*Juglans*).

A **mixed bud** is one that contains each flowers and leaves. When

a bud of this type unfolds, there is produced a leafy shoot which either (*a*) terminates in a flower cluster, or (*b*) bears flowers or flower clusters in the leaf axils. The first-mentioned type of mixed bud is characteristic of the fruits (Fig. 10), apple, pear, blackberry (*Rubus*), raspberry (*Rubus*), and grape (*Vitis*), and many others; whereas the second type is found in such plants as the persimmon (*Diospyros*), mulberry (*Morus*), fig (*Ficus*), oak (*Quercus*), avocado (*Persea*), and a number of others.

It is rarely possible to distinguish leaf from fruit or mixed buds by their external appearance. In the apple, the mixed buds are thick and rounded, whereas leaf buds may be distinguished because of the different positions which they occupy with reference to the stem. In plums, for example, the fruit buds usually stand out at an angle of about 30 degrees, while leaf buds are appressed to the stem.

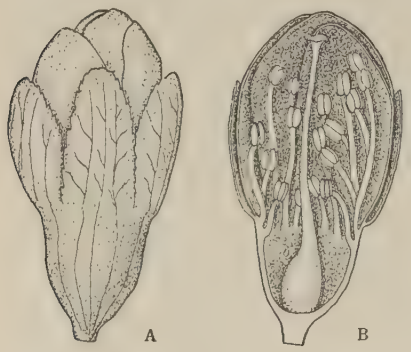


Fig. 9.—Flower buds of plum. *A*, external view; *B*, lengthwise median section.

Buds may be classified, as **to their development,** into (*a*) **active** and (*b*) **dormant** buds. An active bud is one which develops into a new branch stem or (in the case of terminal buds) into an elongation of an already existing stem. Dormant buds are ones which remain undeveloped. The terminal bud of a branch as noted above, in most trees and shrubs, is almost always the most active and grows more vigorously than any of the axillary buds. The latter generally decrease in activity the further they are from the terminal bud. Those buds which are several internodes distant (varying with species and with conditions) from the apex of the stem, are dormant and normally do not develop at all into branches. In most plants the removal of a terminal bud or of the upper end of a branch stem increases the activity of the remaining axillary buds and as a result some of the dormant buds may become active. This "awakening" of dormant buds by the removal of the terminal part of the stem is less complete the further the buds are down the stem. Thus it may be said that the degree of activity of active buds decreases and the "depth" of dormancy of dormant buds increases the greater the distance from the end of the branch.

Many buds which are apparently adventitious are often in reality

axillary buds which have remained dormant for so long that their original position relative to a leaf, long since shed, is difficult to determine.

The branching system of the shoot is largely determined by the arrangement of the buds. If the bud arrangement is alternate, opposite branching cannot occur. Similarly whorled branching will not be found in plants with opposite or alternate bud arrangement. It does not follow, however, that branches will always occur two at a node in a plant having two buds at a node.

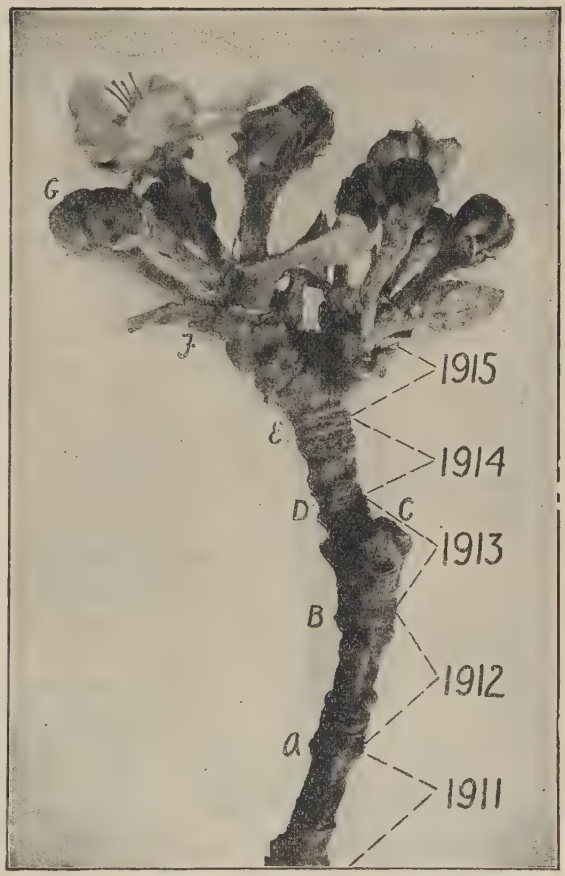


FIG. 10.—Fruit spur of apple. Two opened terminal buds are shown. These terminal buds are mixed buds. (After Robbins, from *Botany of Crop Plants.*)

Not all of the leaf buds on a stem develop. Many remain dormant while others make a short growth and then die as the result of insufficient nutrition or of the attacks of insects or disease. There is competition among the different buds and young branches for light and for food materials and the less vigorous active buds and young branches may fail to develop further. Not all the axillary buds are leaf buds. One or more at a node may be fruit buds which do not develop into permanent branches. On these various accounts branches are much less numerous than axillary buds and branching is much less constant and regular than is bud arrangement.

It is a common and well-known practice of orchardists and gardeners to change the form of plants while they are still young by pruning, which is the judicious removal of buds or branches. The removal of terminal

buds or terminal portions of branches will stimulate the development of axillary buds, cause a spreading of the plant, and thus produce a broad tree with a "low head." A cylindrical or pyramid type of tree may also be secured, by removal of a certain number of lateral buds or branches. Thus it is that by the removal of buds, and branches, a tree or shrub may be forced or "trained" to assume any desired form.

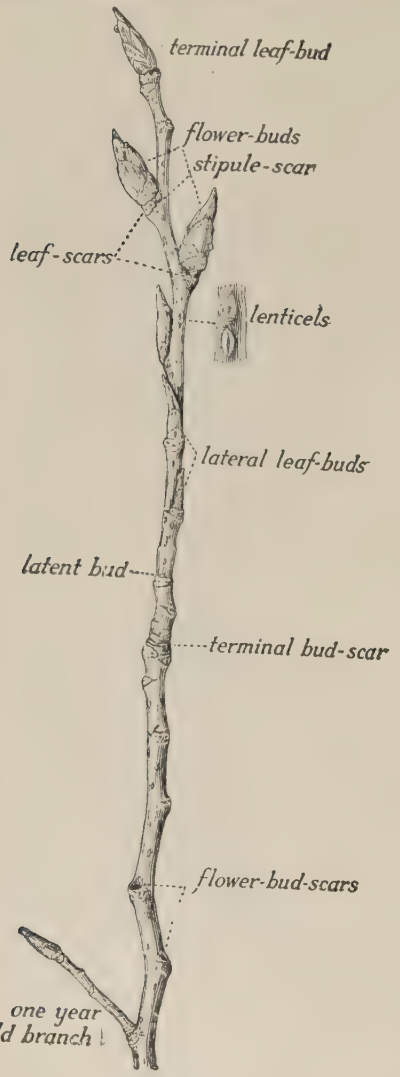


FIG. 11.—Two-year old cottonwood twig. (From Robbins' *Botany of Crop Plants*, after Longyear.)

The Stems of Woody Deciduous Plants in their Winter Condition.—Most orchard trees, ornamental trees and shrubs and forest trees, except pines, firs, spruces and other gymnosperms, are deciduous, losing their leaves in the fall and remaining bare of leaves for some months each year. Such plants in their leafless winter condition are particularly favorable for the study of branching, various types of buds and other features of the shoot. A several-year old twig of such a plant (cottonwood) is illustrated in Fig. 11. At the tip is the large terminal bud and at each node an axillary bud. If the brown bud scales are removed from the terminal bud or certain lateral buds young overlapping foliage leaves may be found within. In the spring, the short internodes within each active bud will elongate, thus bringing the rudimentary leaves out of the bud and adding to the length of the main twig or branch (if it is a terminal bud) or producing a new branch. Within some of the axillary buds partially developed flowers may be found.

Below each bud is a semi-circular to elliptical **leaf scar.** This was

left when the leaf, in the axil of which the bud was formed, detached itself from the twig. The number of these scars at a node shows whether the leaves were alternate, opposite or whorled in arrangement. If a hand lens is used one may find within each leaf scar a number of slightly raised areas. These are the **bundle scars** left where the conducting strands passing out from the stem into the leaf stalk were broken off when the leaf fell.

In such a twig the growth in length during each of the last few years can be easily determined, for a ring of **bud scale scars** marks the end of one year's growth and the beginning of the next. When the closely set bud scales of a terminal bud fall off in the spring they leave a number of scars so close together as to form a distinct ring. Thus the growth of the last year is the length of stem between the present terminal bud and the first ring of scars, unaccompanied by buds, where the bud scales of the terminal bud fell off last spring. The growth of the year before last is that portion of the length of the stem between the ring of bud scale scars nearest the terminal bud and the next lower ring. The spacing of these rings often reveals striking differences in the amount of growth produced each year, for there is practically no increase or decrease in the length of any portion of a stem after that portion is a year old.

On some twigs flower bud scars may also be found where the short branch which developed from a flower bud became detached from the stem after the fruit had matured.

Close examination of the twig surface where there are none of these various kinds of scars will reveal numerous lighter colored, slightly raised spots on the bark. These are **lenticels,** regions which permit the passage of gases inward and outward. Except for these lenticels the bark would very effectively prevent the passage of air and also the loss of water from underlying stem parts.

Different Kinds of Stems and Roots.—The roots, stems, leaves and flowers are not always typical, but may be modified in some cases to such an extent as to be scarcely recognizable. For example, the tendril of the garden pea (*Pisum sativum*) is a leaf part, morphologically; the Irish potato tuber, a modified stem and the sweet potato, a modified root.

Some seed plants do not possess all of the usual parts of the plant body, namely, roots, stems, leaves and flowers. For example, in the common water bladderwort (*Utricularia vulgaris*) the roots are wanting; in the floating *Wolffia*, both leaves and roots are absent; and in *Rafflesia arnoldii*, a tropical parasite, which has the largest flowers of any plant in the world, the plant is reduced to a flower and a mass of undifferentiated cells within the tissue of the host.

The stems may be in the air (aerial) or underground (subterranean). The stems of most seed plants are aerial. However, in such plants as common Irish potato and Canada thistle there are stems underground as well as above ground.

We may classify the various kinds of leaves of seed plants as follows:

1. Vegetative leaves, including
   - (*a*) Ordinary green foliage leaves
   - (*b*) Scale leaves, such as the scales of a bud
   - (*c*) Bracteal leaves, such as the small leaves (bracts) in the axils of which flowers are borne.
2. Floral leaves (sepals, petals, stamens, carpels).

Ordinary plants have soil roots but there are some plants that have roots which grow in the air or the water. Duckweed (*Lemna*), a small plant which grows floating on the surface of water, has water roots. Air roots occur in many plants such as Virginia creeper (*Ampelopsis*), some tropical orchids, banyan tree and other species of *Ficus*. On the banyan tree the air roots are often very large, and arise from branches far above the ground. They grow downward, and when they touch the ground, become firmly attached, and act as a support or prop to the heavy branches. The aerial roots of epiphytic orchids possess a peculiar tissue capable of absorbing moisture from the air.

In addition to the ordinary underground (soil) roots of corn, this plant develops aerial (air) roots at the nodes, the so-called **prop** or **brace** roots.

Factors Concerned in the Orientation of Different Parts of the Plant Body.—*Geotropism.*—The main stem of most plants tends to grow vertically upward and in those plants which have a single primary or tap root that root tends to grow vertically downward. As a result, the direction of growth of the main stem and the tap root is generally at right angles to the surface of the ground. However, in the case of plants growing on a steep slope it is clear that the stem is not at right angles to the surface of the soil but that it tends to be truly perpendicular, that is, parallel to the radius of the earth at the spot where it stands. Regardless of the slope of the land the tap root also tends to grow perpendicularly but in the opposite direction from the main stem.

When a seedling plant, or an older plant having a single primary root and one main stem, is placed in a horizontal position the growing region of the root will bend until it points downward and the growing portion of the stem will curve upward. (Fig. 12 A-B.)

The stimulus, which is responsible for the tap root growing straight downward and for the main stem growing perpendicularly upward and

which causes these organs to bend back into the perpendicular when displaced from that position, is gravity. This adjustment of the parts of a plant relative to the direction of gravity is called **geotropism.** Organs whose direction of growth may thus be determined by gravity are said to be **geotropic.** It is a very remarkable fact that when a plant is placed in a horizontal position the *same* stimulus (gravity) is responded to by the roots and by the stem with exactly *opposite* **reactions.** Organs which, like the root, bend downward when displaced from their normal position are said to be **positively geotropic** while those which bend upward are spoken of as **negatively geotropic.**

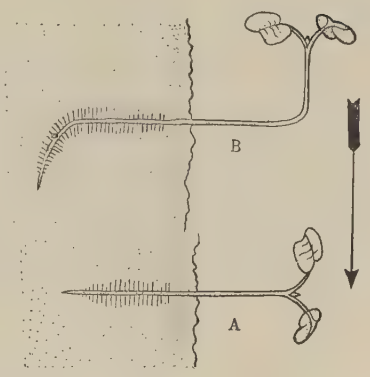


FIG. 12.—Geotropic curvature of a seedling of mustard (*Brassica*). *A*, just after being placed in the horizontal position. *B*, about 24 hours later. The positively geotropic root has bent downward, the negatively geotropic stem upward. (After Sachs.)

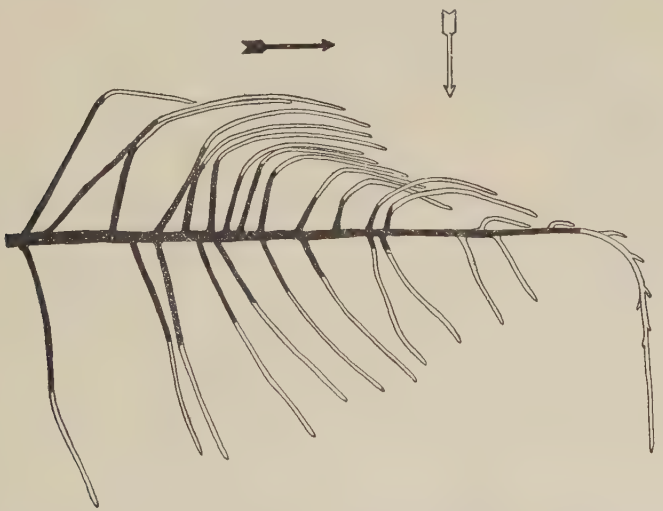


FIG. 13.—Diagram of the root system of the broad bean (*Vicia faba*) showing the plagiogeotropic curvature of the secondary roots as contrasted with the orthogeotropism of the primary root. Originally the whole primary root was growing parallel to the direction of gravity, shown by the solid black arrow. Then the root system was turned through 90° so that it was at right angles to the direction of gravity (outlined arrow). Growth of the root system before and after the change of position are indicated respectively by solid black and outline portions of the figure.

In the case of the primary root and the main stem, the position of rest is parallel to the direction along which gravity acts, but in the case of secondary roots (first branches of a primary root) and the larger branches of the stem of most plants, the position of rest is either horizontal or oblique to the perpendicular. Frequently the position of rest of a secondary root or a branch is at a certain definite angle with the perpendicular. When such a root, for instance, is displaced from this characteristic angle it will tend to bend back into the rest position, curving upward if it has been displaced downward, and curving downward if it has been displaced upward (Fig. 13). The finer branches of the primary root and of the shoot generally are only slightly and sometimes not at all influenced in their direction of growth by gravity.

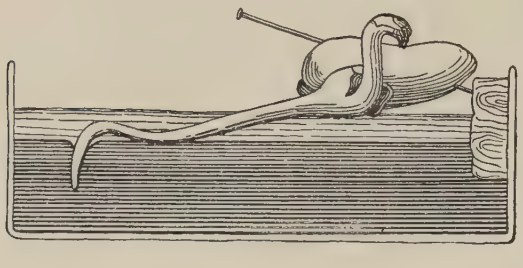


FIG. 14.—Diagram showing penetration of mercury by a downward curvature of the primary root of broad bean (*Vicia faba*). This shows that the geotropic curvature is not a mere passive bending of the root-tip under its own weight. (Redrawn from Sachs.)

Phototropism.—If a house plant is placed at some distance from a window the growing part of the stem will tend to curve toward the light source. It will not actually grow directly toward the light because the gravity stimulus will tend to keep it growing perpendicularly upward. The direction in which it grows will be the resultant of two tendencies of the stem: (1) the tendency to grow parallel to the direction of gravity and (2) the tendency to grow parallel to the direction of the illumination. The adjustment of various plant parts relative to the direction from which light falls upon them is called **phototropism.** The main stems of most plants are **positively phototropic** while the primary roots of a few plants have been shown to be **negatively phototropic.**

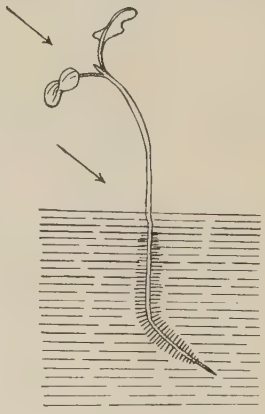


FIG. 15.—Mustard seedling growing in water showing the positively phototropic curvature of the hypocotyl and the negatively phototropic curvature of the root. The arrows show the direction from which light is falling upon the plant. (After Sachs.)

Leaves also are commonly phototropic, but they generally so adjust themselves that the leaf surface is not parallel to, but approximately at right angles to, the direction of the light which falls upon them.

Other Tropisms.—Gravity and light are without question the most important of the external factors which determine in what direction plant parts shall grow. Other such factors are: (1) differences in the quantity of moisture in the medium surrounding the organ in question, (2) differences in the concentration of certain other substances in the medium, (3) differences in temperature in the medium, (4) contact with some solid object, and (5) movement of water in which certain plant organs may be growing.

Hydrotropism.—The accompanying figure shows a simple demonstration of hydrotropism, the effect of differences in the quantity of moisture in the atmosphere upon the direction of the growth of the root. A wide mesh sieve is filled with moistened moss, sawdust, or other loose, water-retaining material in which peas or other large seeds are planted. The sieve is then hung in a slanting position as shown in the figure. When the seeds germinate the radicles grow perpendicularly downward by reason of their positive geotropism and soon grow out into the air through the openings in the sieve. If the atmosphere into which the roots grow is very moist, they will continue their perpendicular direction of growth into the air, the only stimulus affecting the growth of the roots being gravity. However, if the atmosphere in the room where the experiment is being performed is quite dry the root-tips soon after emerging from the moist sawdust or moss will begin to curve toward the surface of the sieve and will then grow along the moist surface. This bending from a region of low-moisture content to one of high-moisture content is called **positive hydrotropism.** It is no doubt of considerable importance to the plant that its roots have the power to curve away from relatively dry regions and grow toward moister parts of the surrounding soil. The frequent clogging of drain pipes by

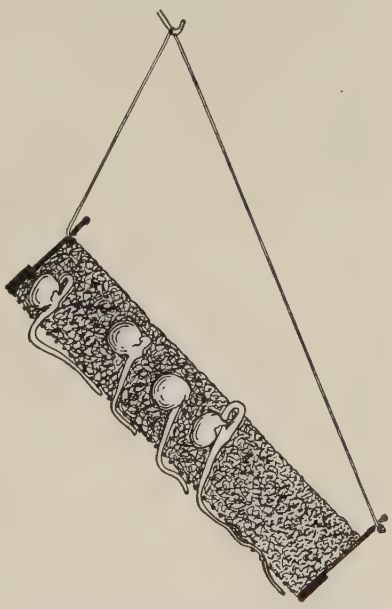


FIG. 16.—Diagram, illustrating the hydrotropism of roots. For explanation see text. (Redrawn from Sachs.)

roots and the greater abundance of roots in moist than in dry soil are not due primarily to hydrotropism, however, but to the fact that the growth and branching of roots are more active when water is abundant than in dry soil.

Chemotropism.—This term is applied to growth curvatures in a direction determined by the stimulus of some substance not uniformly distributed in the soil or other fourth medium. The filaments (*hyphae*) which make up the plant body of many fungi and the tubes which are developed by germinating pollen grains furnish better examples of chemotropic curvatures than do roots.

Thigmotropism.—The tendrils, by means of which such plants as the squash (*Curcurbita*), the wild cucumber (*Echinocystis*), and the grape (*Vitis*) attach themselves and climb over other plants, are sensitive to contact. When one side of such a tendril comes into contact with a solid object the tendril curves so that the stimulated side becomes concave. If the object is of small diameter this curvature of the tendril continues until it has several times encircled the support. Such curvature in response to contact is called *thigmotropism*.

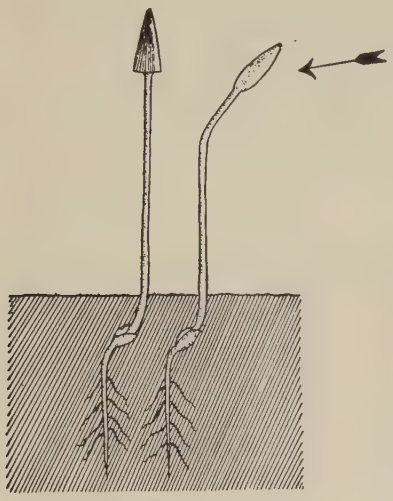
Stimulus, Perception, Transmission, Reaction.—These various tropisms illustrate a property of protoplasm which has not yet been mentioned. That is the property of irritability. By the term irritability, used in this connection, we mean the power of living things to respond in a characteristic way to various external conditions.

Clearly such responses to external stimuli as have been described above in the account of the tropisms must involve at least two processes, (1) the **perception of the stimulus,** be it gravity, difference of illumination or other stimulus and (2) **the reaction of the plant** which in the case of the tropisms is a curvature resulting from a more rapid growth of cells on the convex side than on the concave side. In many cases these two phases take place in different parts of the reacting organ and in such cases there must clearly be a third phase, that of transmission from the region which perceives the stimulus to the region or zone which reacts to the stimulus.

The young shoots of germinating oats, wheat, millet, sorghum, and other grasses are positively phototropic. In millet and sorghum the curvatures which result when the seedlings are lighted mostly from one side take place some distance below the tip of the shoot. This reacting zone, even though itself in darkness, will bend when the extreme tip is stimulated by light. This can easily be shown by placing little caps of opaque paper or tin foil over the tips of the shoots. When this is done the shoots do not curve although other seedling shoots, without " light shades " over the tips, will show phototropic curvatures even though

all but the tips be shaded. In such cases the light stimulus is perceived by one part of the organ and is then transmitted through a region incapable of either perception or reaction to a third zone where the curvature is executed.

Similarly, in the case of geotropic roots, the extreme tip is the region which is sensitive to the stimulus of gravity, but it is in a zone



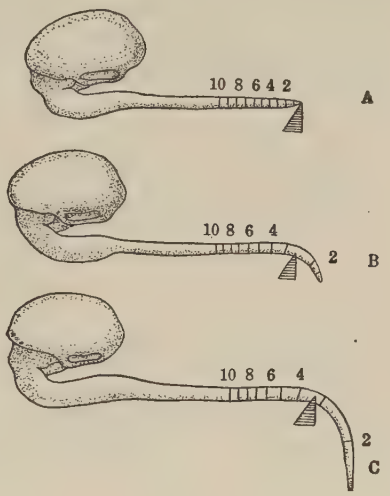


FIG. 17. FIG. 18.

FIG. 17.—Diagram showing that the region of light perception and that of reaction to light stimulus in the seedling of millet (*Setaria*) are at some distance from each other. In both seedlings the region of reaction is illuminated but in the case of the seedling to the left the light sensitive tip is shaded by an opaque paper cap. (Redrawn from Sachs.)

FIG. 18.—A seedling of white lupine (*Lupinus albus*) at the time it was placed in the horizontal position (*A*), and after a shorter and longer period (*B* and *C*) in the new position. The end of the root is marked off into zones beginning with the extreme tip of the root and each originally one millimeter long. Note that the region of curvature corresponds with the region of most rapid elongation and that the sensitive region (included in the first two millimeters) does not elongate much during the curvature. (Redrawn from Sachs.)

some distance behind the tip that the curvature takes place. Czapek showed this clearly when he caused roots to grow into sharply bent-glass tubes so that the sensitive root-tip was forced to bend at right angles to the rest of the root. In the case of such roots no curvature took place when the tip pointed downward, even though the rest of the root, including the region capable of reaction, was kept horizontal;

however, when the tip did not point downward a geotropic curvature took place even though the rest of the root was in the position of rest (Fig. 19).

Importance of the Tropisms in the Life of the Plant.—Clearly the negative geotropism and positive phototropism of the stem are advantageous to the plant since they result in the stem growing upward and thus cause the leaves to be favorably placed for the performance of their functions. The more or less horizontal position of the leaves which results in part at least from their phototropic reaction is also of obvious advantage to the plant. Similarly the positive geotropism, positive hydrotropism, and also perhaps negative phototropism, of the

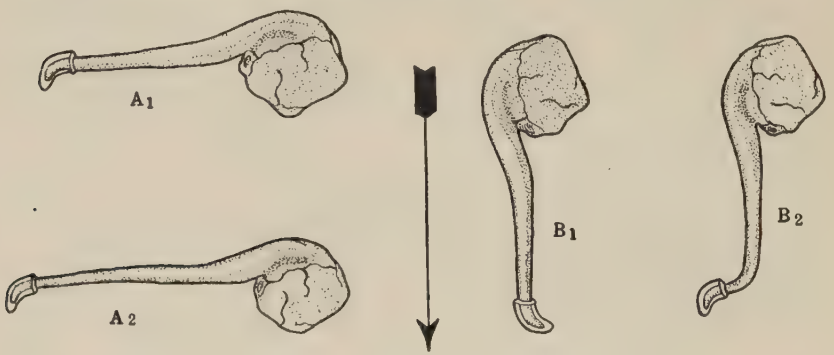


FIG. 19.—Diagram illustrating Czapek's experiment showing the separation of the sensitive and reacting zones in the root of the white lupine. Explanation in the text. A_1 and B_1 show roots at the beginning of the experiment. A_2 and B_2 shows the same seedlings several hours after being placed in the positions shown in A_1 and B_1. The arrow indicates the direction of gravity.

seedling root combine to direct that organ downward into the soil where its functions can best be carried out.

A further illustration of the advantage to plants of certain tropisms is furnished by the recovery of the normal position by grain which has "lodged" because of heavy rains or high wind. Such lodged grain is at first prostrate on the ground or semi-prostrate. If the plants are not too old, geotropic curvature takes place at the nodes, and the upper parts of the plants are thus brought again into the normal, perpendicular position. In the case of wheat, oats, barley, and other grains the stem is surrounded just above each node by a thick cushion of thin-walled tissue which is really part of a leaf base. As long as the stem remains perpendicular this tissue does not grow. However, when the stem is placed in a horizontal position or is much removed from the perpendicular, the tissue of the underside of this cushion is stimulated

by gravity to renewed growth so that the stem is bent upward at that place and the upper side of the cushion somewhat compressed (Fig. 20). If several such cushions react thus, the upper part of the shoot may be brought into the normal position. It is an interesting fact that if the stem is rotated around a horizontal axis at a constant speed the cushions of tissue will start to grow on all sides and will as a result increase considerably in length.

Heredity and Environment.—The plant is a working, living machine with structures for carrying on its various life activities. It is well to keep in mind that the way the plant is constructed and the manner in which it does its work are determined by its inheritance on the one hand, and by the environment in which it lives on the other. The general shape and structure of an apple leaf, for example, is pretty well determined by inheritance; but slight variations in the shape and thickness of the leaves may be due to the influence of environmental factors, such as moisture and light.

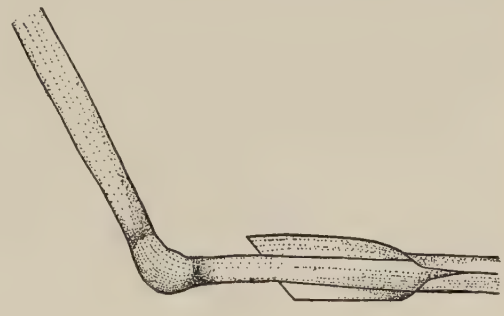


FIG. 20.—A "lodged" grass stem showing the upward bending at the node resulting from the geotropic reaction of the cushion of tissue around the node.

Although the environment has a marked effect upon the structure and behavior of living things, the effect is always limited by the inherited tendencies of the organism. It appears that certain structures of the plant are more susceptible to environmental changes than others. For example, leaf structure seems to be more responsive to the light and conditions of atmospheric moisture than is flower structure. Again, it is much easier to control a function like water loss from the leaves than it is the function of reproduction. Hence, the plant comes into the world with certain inherited structures and ways of living, and it is well that we know these and reckon with them; on the other hand, the plant is subject to some change—can be trained, so to speak—and such change may be brought about by modifying the conditions under which it lives. The problem of the grower of plants, then, is just this: to know the plants he is growing, their inherited structures and activities; to know the environmental factors operating upon the plants; and to seek to find out what environmental factors will give him the desired

response on the part of the plant. The response may be expressed in boxes of fruit, in pounds of tubers, in size of flower, in flavor of fruit, or in percentage of protein in grain; but whatever the particular response on the part of the plant may be, it is one of his chief problems to find out just what temperature, light, moisture, soil, and other conditions will give the desired response.

The plant, then, is a living thing, with various parts and organs definitely organized into a body, and this body is living in a world by which it is influenced in a great variety of different ways.

The Life Cycle.—By life cycle in the plant is meant that series of changes through which it passes in the course of its development. Every plant, like every animal, begins its life as a single cell. In the simplest plants like bacteria and certain blue-green algae, this single cell is the individual plant itself. It divides, resulting in two individual one-celled plants; these in turn grow and divide, and soon the progeny of the single one-celled plant reaches into the hundreds. The **life cycle** of such a plant is short and simple. In the higher plants like wheat (*Triticum*), the beet (*Beta*), and the apple (*Malus*), the life cycle is much more complex and of longer duration.

According to the length of the life of the individual plants, they may be divided into annuals, biennials and perennials.

An **annual** is a plant which completes its life cycle within one year's time and then dies. For example, in wheat, which is an annual, the seed germinates, the roots, leaves and stems are produced, and in one season the plant reaches adult size; after this relatively brief period of vegetative activity, flowers and seeds develop and within each seed there is a miniature wheat plant, the embryo of the seed. Thus the cycle is complete. In cool climates, certain plants behave as **winter annuals.** In these the seeds germinate in late summer or fall, the young plants live throughout the winter and send up flower stalks and bear seed the following spring.

A **biennial** is a plant which completes its life cycle within two years and then dies. The beet plant may be taken as a type of such plants. The embryo plant resumes its growth at germination of the seed, and during the first season produces a number of large leaves crowning a fleshy root which we call the "beet." Flowers and seed are not produced normally the first year, as in the wheat plant. The plant during the first year is engaged chiefly in storing food in the root. In the fall, the leaves die but the "beet" (root) remains alive. In temperate climates, the beet must usually be dug and stored where it will not freeze during the cold season. The next season the "beet" is set in the ground and it sends up a branched stem to a height of three of four

feet, which gives rise to flowering branches. Seed is finally produced, and soon afterward the plant dies. As in the case of the wheat plant, the beet plant has but one period of seed production, after which the whole plant dies, but the beet requires two vegetative seasons to complete its cycle, whereas the wheat plant requires but one.

There are a number of flowering plants in which at least for a part of the life cycle, the internodes remain very short so that the leaves form a cluster or **rosette** near the ground. This is very common among winter annuals and biennials, such as shepherd's purse (*Capsella*), and certain evening primroses (*Oenothera*). This rosette habit occurs also among certain perennials, such as the dandelion (*Taraxacum*) and many alpine plants.

All the familiar trees and shrubs are good examples of plants which live more than two years. Thus in the apple, after seed germination, there is a succession of growth periods during which there is no production of flowers and seed. At an age of four or five years, depending upon the variety of apple, the methods of pruning, and the environmental conditions, flowers and seed are produced. However, even though seeds are produced, the vegetative activity of the plant continues year after year and both vegetative organs (roots, branches, and leaves) and reproductive organs (flowers and seeds) are produced. Though in the apple, flowering seldom occurs in seedlings until three or four years after seed germination, there are many plants which blossom the first season and yet live for many years. All plants which live more than two years are called **perennials.**

Vegetative activity necessarily must precede reproductive activity. In all plants there is a period, of varying length, when the plant is accumulating food apparently in preparation for reproduction. In annuals and biennials, under normal conditions, the plant dies after producing seed. In these it would seem that the plants' activities were directed toward the production of progeny. However, in many perennials this is not apparent, for in some plants, like the birches and willows, flowers appear before leaves in the spring of the year. But in this case, as in annuals and biennials, the flowers and seed are produced at the expense of food made by leaves and stored in some part of the plant. The nourishment which is used by the birches and willows, for example, in their production of flowers and seeds early in the spring before leaves are formed, was made and stored up by the plant during the previous growing season.

So it is that, in perennial plants, periods of vegetation and reproduction alternate. The vegetative period is usually comparatively long, whereas the reproductive period is brief.

Certain environmental factors may considerably alter the duration

of these periods. For example, favorable temperature and an abundance of water and of available nitrogen in the soil tend to prolong the vegetative period; and, on the other hand, unsuitable temperature conditions, a scarcity of water, and a deficiency of nitrogen in the soil tend to shorten the vegetative period and hasten the time of flowering and seed production.

CHAPTER III

THE CELL

Introduction.—If we cut a thin slice from a root, stem, leaf or any other living plant structure and examine it under the microscope we find that it is made up of many small chambers separated from each other by walls which are generally thin and generally transparent. More careful study reveals that within each of these cavities there is a small quantity of a viscous, almost transparent substance. This is **protoplasm,** the living material of the plant. These masses of protoplasm with their surrounding walls are called **cells.** Cells are in fact the units of structure and function in all organisms. They vary greatly

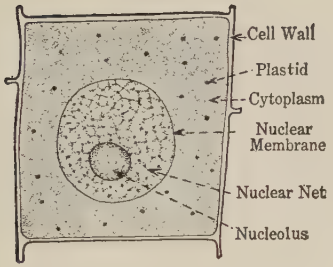


FIG. 21.—A cell from the tip of a root of onion (*Allium cepa*).

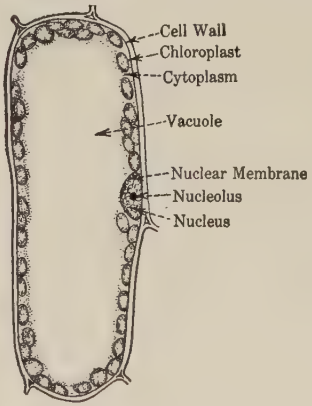


FIG. 22.—A cell from the palisade parenchyma of a leaf.

in size but in relatively few cases is the longest diameter greater than 0.25 millimeter, or less than 0.025 millimeter. Plant cells also differ greatly in shape, in the thickness of their walls, and to a certain extent in the nature of the material of which the walls are made. The structures which are found within the protoplasm are far from uniform in number, form, and size. The three principal parts of the cell will be discussed in the following order:

The Cell Wall
The Protoplast
The Inclusions.

In the previous chapter there was inserted a brief discussion of the two kinds of pure substances, elements and compounds, and of the unit particles, atoms and molecules, of which pure substances are composed. It is necessary at this place to extend that discussion somewhat and to take up a number of other physical and chemical conceptions essential to an intelligent understanding of an account of the composition and physiology of the cell.

Essential Elements and Chemical Symbols.—Of the known elements, about ninety in all, the nine most abundant make up 98 per cent of the earth's crust. The remaining elements, about eighty, constitute approximately 2 per cent. There are listed below some of the more familiar elements. Those in the first column are the nine most abundant. The ten elements printed in italics are those which have long been recognized as essential to the normal development of seed-bearing plants. There is considerable evidence, however, that several other elements, for example manganese and boron, are also essential. Opposite each element in the list is placed the corresponding symbol. These symbols are international in their use and each one is an abbreviation of the English or Latin name of the corresponding element.

Oxygen	O	*Nitrogen*	N	Gold	Au
Silicon	Si	*Sulphur*	S	Iodine	I
Aluminum	Al	*Phosphorus*	P	Lead	Pb
Iron	Fe	*Carbon*	C	Manganese	Mn
Calcium	Ca	Argon	A	Mercury	Hg
Sodium	Na	Barium	Ba	Nickel	Ni
Potassium	K	Bromine	Br	Platinum	Pt
Magnesium	Mg	Chlorine	Cl	Silver	Ag
Hydrogen	H	Copper	Cu	Boron	B

Chemical Formulae and Chemical Equations.—Instead of writing out the full name of a compound, its formula is often used. The formula of a compound consists of the symbols of the different elements of which it is made up placed one after the other. When more than one atom of any element is present in a single molecule of the compound the number of atoms of that element in the molecule is indicated by a figure placed just after the symbol of that element. Thus the formula for water is H_2O, which shows that a molecule of water consists of two atoms of hydrogen and one of oxygen. The formulae of several other common compounds are given below.

Carbon dioxide	CO_2	Sodium bicarbonate (baking soda)	$NaHCO_3$
Sodium chloride (common salt)	$NaCl$	Cane sugar	$C_{12}H_{22}O_{11}$
Sulphuric acid	H_2SO_4	Acetic acid (acid of vinegar)	$C_2H_4O_2$
Calcium nitrate	$Ca(NO_3)_2$	Stearin (a fat)	$C_{57}H_{110}O_6$
Potassium hydroxide (potash lye)	KOH	Haemoglobin (a protein)	$C_{758}H_{1203}N_{195}S_3FeO$

When one or more substances undergo a chemical change with the formation of different substances the process is spoken of as a **chemical reaction**. It is convenient to represent such a reaction in the form of an equation, giving on the left-hand side the original substances and on the right-hand side the products of the

reaction. For instance the reaction which takes place when the element sodium comes in contact with water may be written as follows:

$$2H_2O+2Na=2NaOH+H_2,$$

which means that two molecules of water plus two atoms of sodium react with the formation of two molecules of soda lye plus a molecule of hydrogen. When a solution of common salt and one of silver nitrate are mixed a white insoluble substance, silver chloride, is formed. The equation for this reaction will serve as a second illustration of the use of chemical equations.

$AgNO_3$	+	NaCl	=	AgCl	+	$NaNO_3$
Silver nitrate		Sodium chloride		Silver chloride (insoluble)		Sodium nitrate.

Carbon Compounds.—The element carbon is remarkable for the great number and variety of compounds which it forms with other elements. In fact as many as two hundred thousand different compounds of carbon are known. Most of them are relatively complex and exist in nature only as the products of living plants and animals. A number of the simpler of such compounds have already been made in the laboratory and it is not unlikely that we shall eventually be able to produce artificially many of the more complex ones. Among the thousands of carbon compounds many groups of somewhat similar ones are recognizable, such as the alcohols, organic (carbon containing) acids, etc.

Carbohydrates, Fats and Proteins.—Three groups of substances which include carbon compounds of very great importance to both animals and plants are the carbohydrates, fats and proteins. It is only possible here to give a few of the more general characteristics of each of these groups of compounds and to name a few examples.

All **carbohydrates** consist of carbon, hydrogen, and oxygen. No other elements are found in them. The oxygen and hydrogen are generally present in the molecules of carbohydrates in the same proportions as in water, that is, one atom of oxygen to two of hydrogen. The carbohydrates include the sugars (grape sugar—$C_6H_{12}O_6$, cane sugar—$C_{12}H_{22}O_{11}$, and many other sugars), starch and cellulose. The latter two may be represented by the same formula, $(C_6H_{10}O_5)_n$. In the case of starch and cellulose, as is frequently true among carbon compounds, the difference between the compounds rests not upon any difference in kind or number of atoms present but upon different arrangements of the atoms within the molecules.

Fats also contain carbon, hydrogen and oxygen atoms in their molecules. In the arrangement of the atoms they are very different from carbohydrates. Fats are very abundant in the seeds of cotton, peanut, coconut, corn and flax but are present in all living cells. Palmitin ($C_{51}H_{98}O_6$) and stearin ($C_{57}H_{110}O_6$) are examples of fats.

Proteins are very complex carbon compounds containing, in addition to carbon, hydrogen and oxygen, the elements nitrogen and sulphur. Some proteins also contain phosphorus. Gelatine and egg white consist almost entirely of proteins.

Mixtures.—A quantity of matter in which more than one kind of molecule is present is spoken of as a mixture; that is to say, any material consisting of two or more pure substances not united into a compound is a mixture. The elements in a compound, it will be recalled, are always present in certain definite and constant proportions, but a mixture may vary greatly as to the proportions of its constituents. Mixtures are of two principal kinds: **true solutions** and **heterogeneous mixtures.**

Solutions.—If a small quantity of the pure substance, sugar, is added to the pure substance, water, and the container is shaken or its contents stirred, the sugar disappears. As the sugar goes into solution in the water, the sugar molecules become separated from one another and uniformly distributed through the water. The largest particles in such a true solution are molecules; and since molecules are too small to be seen with even the highest power of the microscope, the different constituents of a true solution can not be distinguished by the eye.

A true solution differs from a compound in two respects: first, in that it consists of at least two kinds of molecules; and second, in that the proportions of the components may vary. Thus sugar solutions may contain any concentration of sugar from only a trace to a hundred parts or more to one hundred of water.

The different substances making up any solution are spoken of as the **components** of the solution. When one of the components is water or some other liquid, it is often spoken of as the **solvent**, while the components which are dissolved in the solvent are spoken of as **solutes**. In most solutions water is the solvent. The solute may be a solid substance, such as salt or sugar, other liquids such as alcohol, or a gas. "Soda water" is a solution in which water is the solvent and carbon dioxide the solute.

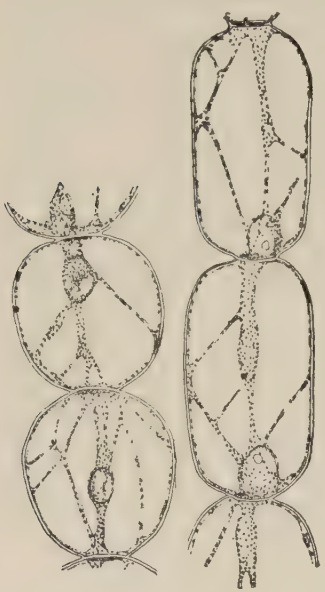


FIG. 23.—Cells from the stamen hairs of *Tradescantia*, showing strands of cytoplasm across the vacuole.

Most solutions are liquid, but there are also solutions (air, for example) of gases and solid solutions.

Heterogeneous Mixtures.—If the particles of one or more of the substances in a mixture are larger than molecules the mixture is a heterogeneous mixture. A piece of granite is an example of such a mixture, consisting of particles of different kinds of rock clearly distinguishable by the naked eye. Similarly a mixture of white sand and sugar is a heterogeneous mixture. The particles can be readily distinguished by the use of a lens or a microscope, and are many times larger than molecules.

Colloidal Solutions.—A peculiar kind of heterogeneous mixture, which is of great interest especially to botanists and zoologists, is the colloidal solution. In most colloidal solutions one or more of the components is mixed with a liquid and is in so fine a state of division (as tiny solid particles or as droplets) that it settles out, if at all, very slowly. The suspended particles of a colloidal solution may be too small to be seen by the most powerful microscopes but are *larger than molecules*. In such cases a colloidal solution may appear perfectly clear like a true solution. If an intense beam of light is passed through a colloidal solution, however, the path of the beam will be distinctly visible where it passes through the solution. This is due to the fact that the colloidal particles in suspension are large enough so that they appreciably scatter the light just as do dust particles when a beam of light enters a darkened room. If a true solution, for example, salt in distilled water, is used, the path of the light through the solution will not be visible be-

cause the particles of dissolved substance are not large enough to scatter light to an appreciable extent.

Familiar examples of colloidal solutions are egg white, glue or gelatine mixed with water. Even such substances as common salt, which form a true solution with water, may form a colloidal solution in some other liquid. When a substance such as dry glue is placed in contact with water, with which it can form a colloidal solution, it absorbs the liquid and swells. This absorption of water with attendant swelling is spoken of as *hydration*. As the result of hydration, a jelly-like colloidal mass, called a *gel*, is formed. In many cases as more and more water is absorbed the gel becomes a liquid. In this condition it is spoken of as a *sol*. Gelatine can take up by hydration thirty to forty times its weight of water and still remain a gel. Lowering the temperature of a sol may change it into a gel and vice versa, as when a pot of glue is heated or allowed to cool. Some sols are changed by heat or certain chemicals into gels and can not be changed back to sols again.

The relation of some of the subjects just discussed to the structure and functions of the cell may be made clearer by the following statements in which some of the terms explained above are used. The protoplast of a plant cell is generally surrounded by a wall composed of the *compound*, cellulose, whose molecules are made up of *atoms* of the *elements*, carbon, hydrogen and oxygen. Everything that enters the plant cell must be in the form of a *true solution* for substances in *colloidal solution* can not pass through the wall or enter the cytoplasm. The cytoplasm itself is a colloidal solution in which many small particles (but larger than most molecules) of proteins and other substances are suspended in a watery true solution.

THE CELL WALL

The wall is secreted by the protoplast which it encloses. Where, as in most cases, the wall separates the protoplasts of two cells, it is produced in part by each of these two masses of protoplasm. When the cells are young the wall is very thin but as they grow older, successive layers of new cell-wall material are laid down so that the wall may finally come to have a thickness many times as great as when it was first formed. The original thin wall separating two adjacent protoplasts is called the **middle lamella.** It is largely composed of a substance called pectose or of a compound of a related substance (pectic acid) and lime. The rest of the cell wall is made up almost entirely of the carbohydrate cellulose $(C_6H_{10}O_5)_n$. Cane sugar, glucose or grape sugar, and starch are other familiar examples of carbohydrates. The pectose present in large quantities in the middle lamella and in small quantities in the rest of the cell wall easily changes into pectin. Pectin is a substance which causes fruit jellies to stiffen if it is present in sufficient quantities, and if it is accompanied by proper proportions of fruit acid and sugar. Cellulose is a material which is probably of greater economic importance than any other material not used as food by man. Cotton, linen, hemp, and wood consist of pure cellulose or of modified forms of cellulose which will be discussed later. Man is unable

to use cellulose for food, but it can be digested and utilized by cattle and other herbivorous animals. It has also come to be used as a raw material in the chemical industries which produce such substances as guncotton and other explosives, celluloid, and artificial silk.

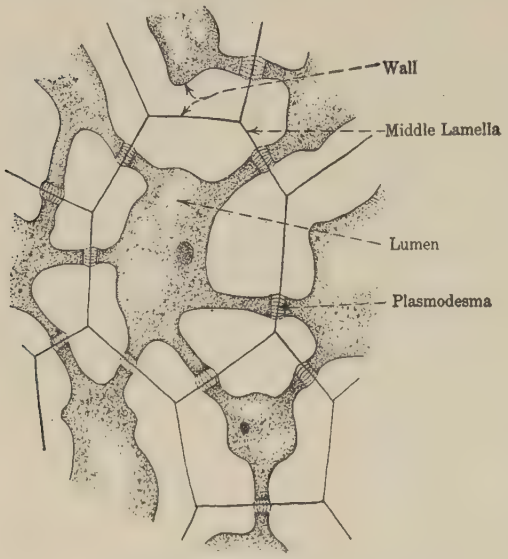


FIG. 24.—Section of endosperm of date seed showing plasmodesma.

THE PROTOPLAST

The term protoplast is a useful designation for the mass of protoplasm, found within a single cell cavity. Each protoplast is a more or less independent unit. However, it has been demonstrated that there are very minute perforations in the walls separating adjacent protoplasts, and that through these openings extend fine threads of protoplasm, called **plasmodesma.**

Protoplasm is not a single chemical compound like the cellulose of the cell wall, but a mixture of many different compounds. These include carbohydrates, water, fatty substances, proteins, and simple compounds of the metals calcium, potassium, and magnesium and of phosphorus, sulphur and iron. With the exception of the water the proteins are present in larger quantities than

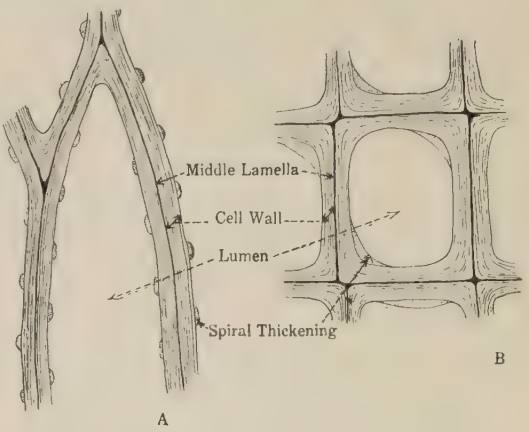


FIG. 25.—A tracheid (dead conducting cell of wood). showing the lumen, which is the cavity formerly occupied by the protoplast, the cell wall and spiral thickening, both originally of cellulose, and the middle lamella. *A*, in longitudinal, *B*, in cross section. (Redrawn from Sharp's *Cytology*, McGraw-Hill Book Co., Inc.)

any of the other substances. Familiar examples of proteins are gelatine and egg white. In addition to carbon, oxygen and hydrogen, the proteins contain nitrogen and sulphur, and in the case of some proteins phosphorus also. The protoplasm generally seems to be of the consistency of a viscous liquid, though in some cells and under certain conditions it is more like a stiff jelly. It consists of particles and drops, mostly too minute to be visible, suspended in a fluid. When a cell dies the protoplasm loses its liquid consistency and coagulates or sets into a firm mass.

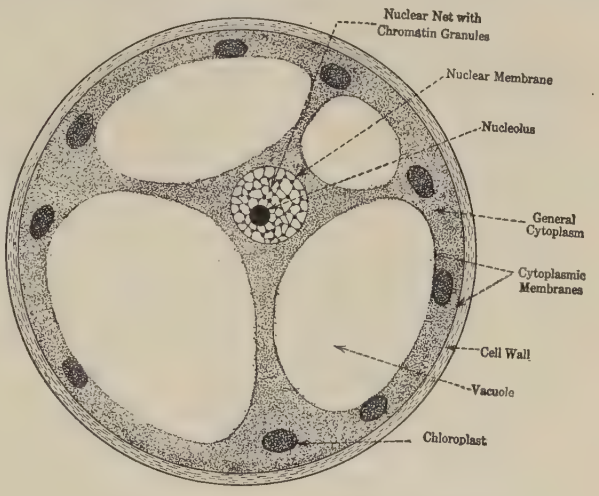


FIG. 26.—Diagram of a single-celled (unicellular) green plant, showing the cell wall, the vacuoles, and the relation of the different parts of the protoplast.

The living material of the cell is not uniform but is differentiated into a number of cell organs and regions. These different parts of the protoplast and their relation to each other are shown in the following outline.

- The Protoplast
  - Cytoplasm
    - Cytoplasmic membranes
    - General cytoplasm including
      - Plastids
        - Leucoplasts
        - Chloroplasts
        - Chromoplasts
      - Chondriosomes
  - Nucleus
    - Nuclear membrane
    - Nuclear sap
    - Nucleoli
    - Nuclear net
      - Linin
      - Chromatin granules.

The Cytoplasm.—In the protoplast of every typical cell there is a round or oval structure called the **nucleus.** All of the protoplasm outside of the nucleus is called cytoplasm. The cytoplasm forms, in most cases, the greater part of the protoplast. Within the cytoplasm non-protoplasmic bodies of a number of different kinds may be found. They are called **inclusions.** The most common of these are the vacuoles,

which may be thought of as drops of a watery solution of various substances embedded in the cytoplasm. Vacuoles vary greatly in size. They sometimes make up half or more of the volume of the cell.

In some cases there may be distinguished at the outer surface of the protoplast, where it is in contact with the cell wall, a thin layer which is not finely granular like the rest of the cytoplasm but clear and highly transparent. Although it is impossible to see such a layer in many plant cells there are other grounds for believing that wherever the cytoplasm is in contact with cell wall, with the contents of the vacuole or with water, there is a surface layer differing considerably from the rest of the cytoplasm. We shall speak of such layers, which are no doubt generally too thin to be visible even under the microscope, as **cytoplasmic membranes.** It is generally assumed by botanists that these layers are **semi-permeable** membranes, that is to say, membranes which will permit the free passage through them of water and some dissolved substances but which prevent, or at least very greatly hinder, the passage of certain other dissolved substances. These cytoplasmic membranes have long been thought to be of great importance because of their supposed control over the entrance and exit of substances into and from the cell. Of the existence of cytoplasmic membranes there is little doubt but as to their properties we *know* very little.

Plastids and Chondriosomes.—In many cells there are specialized cytoplasmic structures (living), called **plastids.** These are generally spherical or ellipsoidal in form and may be considered merely portions of the cytoplasm which are specially differentiated to perform a particular function in the cell. The plastids are of three kinds, differing in color and in the nature of the work which they perform. There are green plastids, which are called **chloroplasts**; colorless ones known as **leucoplasts**; and **chromoplasts,** which may be yellow, brown or red in color. The term **chromatophore** is often used to include all colored plastids. The green color of the chloroplasts is due to the presence of pigments (colored compounds) which may be dissolved out by means of alcohol. Two of these pigments (**chlorophyll *a*** and **chlorophyll *b***), are green while the other two (**carotin** and **xanthophyll**), are yellow. The formulae of these four pigments are:

Chlorophyll *a*	$C_{55}H_{72}O_5N_4Mg$
Chlorophyll *b*	$C_{55}H_{70}O_6N_4Mg$
Carotin	$C_{40}H_{56}$
Xanthophyll	$C_{40}H_{56}O_2$

It is an interesting fact that the presence of the element iron in a plant is essential to the formation of chlorophyll. Because plants deprived of iron failed to form chlorophyll it was formerly believed,

before the composition of chlorophyll was known, that iron must be a component of chlorophyll. As the formulae show, that is not the case. Instead of iron another metallic element, magnesium, is present in chlorophyll.

The quantity and intensity of the green pigments is such as to largely mask the yellow pigments. It is the chloroplasts which give the color to the green cells of leaves and of the young parts of stems. Organs which do not normally possess chloroplasts, such as the tubers of the potato, may develop green plastids when exposed to the light. In such cases leucoplasts which were present in the cells before exposure to light are stimulated to produce pigments and are thus transformed into chloroplasts.

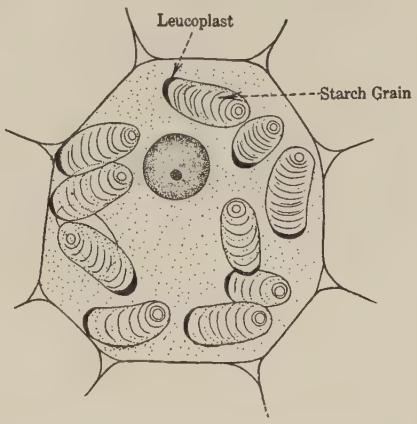


Fig. 27.—Starch-storing cell of *Pellionia* showing leucoplasts and starch grains. (Redrawn from Gager.)

The green plastids are the centers of the process of photosynthesis, by which the simple compounds, carbon dioxide and water, secured from the air and from the soil, are built up into sugar and starch. Leucoplasts are always present in cells in which starch is stored, such as those of starchy seeds, of the potato tuber, and of starch-storing roots like the sweet potato. They are able to change certain sugars (soluble carbohydrates) into starch. The starch is built up inside the leucoplasts into starch grains. As these grains increase in size the leucoplasts stretch to many times their " normal " size.

Chromoplasts are responsible for the red, yellow, or orange color of many flowers and fruits. They owe their color principally to the two pigments, carotin and xanthophyll. However, in many cases the colors of flowers or fruits are due, not to pigments contained in plastids, but to colored substances dissolved in the solution contained in the vacuoles of the cells. A single plastid may be in turn a leucoplast, a chloroplast, and a chromoplast. This is the case in the cells of many fruits, such as the red pepper or tomato. In the young flower of these plants, the ovary, that part of the flower which develops later into the fruit, is almost colorless and the cells near the surface contain numerous leucoplasts. Later, the ovary, as well as the young fruit which develops from it, will become green and chloroplasts will be found to have devel-

oped from the leucoplasts. As the fruit ripens, the chloroplasts are transformed to chromoplasts, and the color of the fruit changes from green to red.

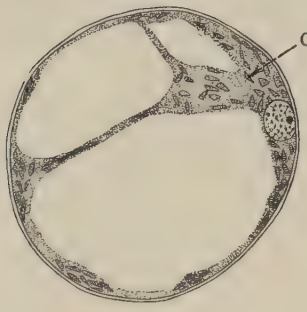


Fig. 28.—Cell from the flesh of a tomato (*Lycopersicum esculentum*), showing the chromoplasts which give the tomato its red color. (After Frank.)

The **chondriosomes** (or mitochondria) are very small bodies having the form of rods, granules, or filaments, which have been found in the cells of many animals and plants. They can sometimes be distinguished in living material but in most cases it is necessary to treat the cells with certain chemicals (fixing agents) and then to stain them before these **chondriosomes** can be clearly seen. The true nature and function of these bodies has been for some years, and still is, a subject of active controversy among cytologists. Many of the persons who have studied the chondriosomes of plants believe that they are structures which develop into plastids. However, since this conclusion is rejected by many and since so many other opinions have been expressed in regard to these structures, it is impossible to make any definite statement as to the part which they play in the life of the protoplast.

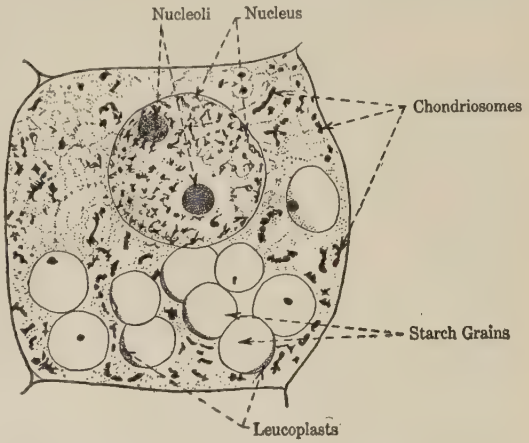


Fig. 29.—A cell from the root of a garden pea (*Pisum sativum*), showing chondriosomes scattered through the cytoplasm. (Redrawn from Mottier.)

The Nucleus.—The nucleus is believed to control all the activities which go on in the living cell and its removal soon results in the death of the cell. There is abundant evidence that it is material within the nucleus which is principally responsible for the inheritance by organisms of the characteristics of their ancestors. Typically the nucleus is a spherical structure, although ellipsoidal, disc-shaped, or considerably elongated nuclei

are often found in plant cells. It is surrounded by a definite **nuclear membrane** and contains a highly transparent watery or slightly jelly-like material called the **nuclear sap.**

Within the nuclear sap are the **nucleolus** (plural, nucleoli) and the **nuclear net.** The nucleolus is another cell structure concerning the function of which cytologists differ. It seems likely that one of its functions is the storage of reserve material of some sort. Usually the nucleus contains but one nucleolus, but two or more may occur in a single nucleus, and in some cases they are lacking altogether. The nucleoli are usually spherical in form. During the division of the nucleus into two nuclei at the time of cell division, the nucleoli disappear entirely and reappear again in the two new nuclei when the process of division is complete.

The **nuclear net** may, in some cases, be quite clearly seen in living cells examined under the microscope. Usually it is necessary to fix and stain the cell before the net can be made out. When the cell is thus treated, certain deeply stained granules are found here and there along the thread of the nuclear net, while the thread itself is found to be very slightly or not at all affected by the staining solution. The material of these granules is called **chromatin** and that of net has been given the name **linin.** It should be borne in mind that these and all the other parts of the nucleus and cytoplasm which have been mentioned, though they may differ in consistency, in staining properties, in chemical composition, and in other particulars, are included under the general term protoplasm. The chromatin is without question a substance of very great importance. There is very conclusive evidence that it is this substance which bears the characteristics which the plant is able to pass on to successive generations. There can be no doubt that the resemblance of a plant to its parents is due to the fact that in the process of reproduction some of the chromatin of each parent plant is contributed to the new individual.

INCLUSIONS

Within the protoplast there are certain non-protoplasmic bodies which are called **inclusions.** These may be drops of liquid, or crystals, or solid bodies of various non-crystalline forms. When they are small it is difficult in some cases to determine whether they are part of the protoplasm or actually non-protoplasmic in nature. The inclusions are (*a*) accumulations of raw materials for food manufacture, (*b*) food, (*c*) by-products and waste materials. They are generally absent in very young cells, but they increase in number as the cells grow older and are particularly conspicuous in cells which serve for food storage.

Vacuoles.—These are inclusions in the form of drops of liquid which are found in all but the very youngest cells. As a young cell grows, its volume increases much more rapidly than does the quantity of protoplasm within it. As a result there is not sufficient protoplasm to completely fill the cell cavity. The water which is absorbed by such cells as they grow makes up the difference in volume. Although the cytoplasm may be somewhat diluted by the absorbed water, much of the latter forms droplets or small vacuoles which are numerous at the time of their first appearance. As the cell grows these increase in size and some of them come into contact with each other and fuse. Thus they become fewer in number but larger in size in the older cells than in the younger ones. By the time the cell has reached its greatest size there is generally only a single large vacuole. This is commonly larger in volume than the protoplasm and occupies the center of the cell so that the protoplast in old cells has the form of a closed sac. In such cells the nucleus lies near the cell wall, embedded in the cytoplasm, or is suspended in the large central vacuole by fine threads of cytoplasm which are connected with the cytoplasm lining the cell wall. In the latter case the nucleus is surrounded by a layer of cytoplasm. It is never in direct contact with the vacuole.

The liquid within the vacuole is not pure water, but is a solution of many substances dissolved in water. Among these substances are the gases of the atmosphere, including nitrogen, oxygen, and carbon dioxide; inorganic salts (such as nitrates, chlorides, sulphates, or phosphates of the metals potassium, sodium, calcium, or magnesium); organic acids (such as malic, formic, acetic, and oxalic acid), compounds of some of these acids with the metals named above; sugars (such as cane sugar, grape sugar, and malt sugar); soluble proteins and simpler nitrogenous compounds; and other substances. The cell sap is generally slightly acid. In the cells of the flowers, leaves, or other parts of many plants, the cell sap contains dissolved **anthocyanin pigments** which give them a red, purple or blue color. The cells of the common red beet owe their coloration to such a pigment dissolved in the cell sap. In the carrot, on the other hand, the yellow color is due to pigments in the chromoplasts. In many colored flowers, though by no means in all, the two methods of coloration are combined.

In addition to vacuoles containing a watery cell sap, there are found in certain cells, oil drops of considerable size which are sometimes spoken of as **oil vacuoles.** They never reach the size of the cell-sap vacuoles of mature cells.

Crystals.—Cells with crystal inclusions can be found in almost all plants. The crystals may be large ones occurring singly in the cells,

or numerous very fine crystals scattered through the cytoplasm and often called **crystal sand,** or bundles of fine sharp needles (**raphides**), or spherical groups of radiating crystals. The crystals are formed in vacuoles, which, in cells containing raphides, have cell sap of a mucilaginous nature. In most cases the crystals are of calcium oxalate. Oxalic acid is a by-product of certain activities of the plant. It is a soluble substance and one which is toxic to the protoplasm if it reaches a high concentration in the cell. When united with calcium, the soluble oxalic acid is converted into the highly insoluble calcium oxalate which can not injure the protoplasm. Needle crystals or raphides are particularly abundant in the cells of plants of the Araceae, the plant family to which the so-called calla lily and jack-in-the-pulpit belong. When a bit of the tissue of either of these plants is taken into the mouth and crushed, there is experienced an intense burning sensation, which is due to the piercing of the mucous membrane by hundreds of these minute crystals. It may be that these needles protect the plants containing them from consumption by snails or other animals. Sometimes the crystals found in living cells consist of calcium carbonate. Protein crystals are also found as inclusions in plant cells as well as non-crystalline protein particles.

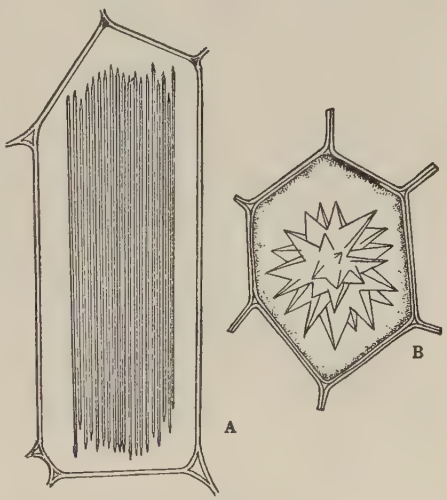


FIG. 30.—Crystal inclusions. *A*, a cell from the stem of spiderwort (*Tradescantia*) showing a group of raphides. *B*, a cell from the leaf-stalk of dock (*Rumex*) showing a cluster of crystals. In *A* the cytoplasm has been omitted.

Starch Grains.—These inclusions are found in green cells after a period of active food-manufacture, and in various food-storing cells such as those of the potato tuber and of many seeds. The stored starch of plants is the most important substance used as food by man. The starch grains which are produced in green food-making cells are formed within the chloroplasts. This starch is called **assimilation starch.** That found in food-storage cells is spoken of as **reserve starch,** and is produced within the leucoplasts. The grains of reserve starch consist of successive layers, which are often thicker on one side of the

grain than on the other. This is conspicuously the case in the starch grains of potato. Sometimes a number of small grains are united into a group which is called a compound grain. Compound grains occur in rice, oats, and some other cereals.

The starch molecule consists of carbon, hydrogen, and oxygen atoms united in the proportions of six of carbon to ten of hydrogen and five of oxygen. Starch grains are insoluble in water. The plant is able to change starch into certain sugars which are soluble and which can pass from one part of the plant to another.

When a green cell which contains assimilation starch discontinues food manufacture, as it does when night comes on, the starch is changed into sugar which passes to parts of the plant where it will be used or stored.

The sugar which reaches the storage tissues may be stored in the cell in the form of sugar or may be converted again by leucoplasts into starch and remain in this form until it is needed by the plant. It is then changed back into sugar and passes to the parts of the plant where it is to be used as food.

When starch grains are treated with a solution of iodine they become blue in color. The form of the grains of reserve starch is different in different plants, a fact which often makes it possible to determine, by microscopic examination of a sample of starch, from what plant it was secured.

HISTORY OF OUR KNOWLEDGE OF THE CELL

Cells were first seen by Robert Hooke, an Englishman, who in addition to being a professor of geometry, an architect, and an experimenter with flying machines, was also interested in optics, and greatly improved the compound microscope. This instrument was invented by the brothers Janseen, spectacle makers of Middleburg, Holland, in 1590. The compound microscope soon became the most important tool of biological science and such it has remained. Hooke, who lived from 1636 to 1703, examined a great number of natural objects with his improved microscope. It was when he placed a small fragment of cork (the dead outer bark of woody plants), under his microscope that he first observed the numerous cavities which we now know to be characteristic of the structure of all plant parts. He gave the name **cells** to the cavities. There are no protoplasts in the cells of cork, and even when Hooke examined slices of living plant tissue the contents of the cells escaped his notice on account of the transparency of the protoplasm and the imperfections of his microscope. The term cell is still, and perhaps

always will be, generally used for the structural units of plants and animals although it is now recognized that the protoplast is the essential part of the cell and that the wall is merely a product of the protoplast. Hooke made no systematic study of the structure of plants. This was first attempted by the Italian professor of medicine, Marcello Malpighi (1628–1694), who published an Anatomy of Plants in 1675, and by Nehemiah Grew (1641–1712), an English physician, who worked out the form of the cells and their arrangements in different parts of the plant. These men did not, however, see the protoplasts of the cells which they studied and had no idea how the cell walls were formed.

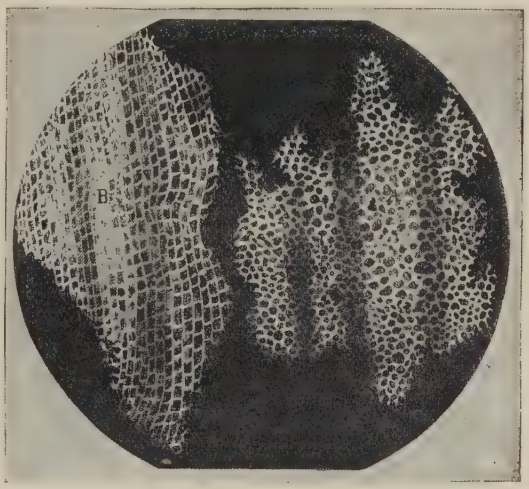
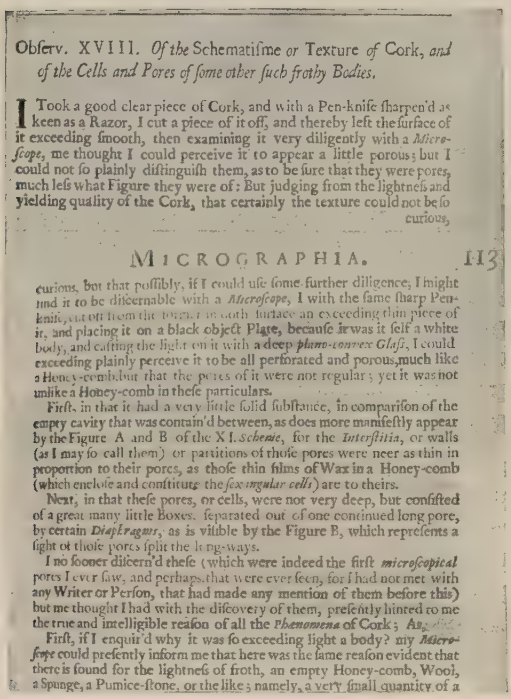


FIG. 31.—Robert Hooke's illustrations of cork cells as he saw them under his microscope. Reduced facsimile reproduction from his *Micrographia* published in 1665.

The Cell Theory.—No incident in the history of our knowledge of the cell is of greater importance than the putting forward of the Cell Theory by Schleiden and Schwann. These two men, the former a botanist who had given up the practice of law to devote himself to the study of the structure and physiology of plants, and the latter a student of animal anatomy, attempted to put into the form of a general statement or theory the facts which they and earlier workers had discovered as to the structure of plants and animals. These two men were friends, and it is said that their theory had its origin in a conversation held between them while they were dining together one day in October, 1838. After their exchange of views at the table Schleiden accompanied Schwann to the latter's laboratory where he examined some of Schwann's microscopic preparations and was struck with the many points of resemblance between the animal cells which he saw there and the plant cells which he had himself studied. Schwann was largely responsible for the publication of the theory which grew out of this and later discussions, but it is doubtful whether the theory would have been put forward at all but for Schleiden's contributions, many of which, it must be said, proved later

to be entirely erroneous. In its main features the theory was correct, but more important than its truth or falsity is the fact that it proved a stimulus to renewed and more thorough research by many students of the structure and development of plants. It marked the beginning of a new epoch in the anatomy of plants and animals. In the words of Schwann, this theory set forth that "the elementary parts of all tissues are formed of cells in an analogous, though very diversified manner, so that it may be asserted that there is one universal principle of development for the elementary parts of organisms, however different, and that this principle is the formation of cells."



Obſerv. XVIII. *Of the* Schematiſme *or* Texture *of* Cork, *and of the Cells and Pores of ſome other ſuch frothy Bodies.*

I Took a good clear piece of Cork, and with a Pen-knife ſharpen'd as keen as a Razor, I cut a piece of it off, and thereby left the ſurface of it exceeding ſmooth, then examining it very diligently with a *Microſcope*, me thought I could perceive it to appear a little porous; but I could not ſo plainly diſtinguiſh them, as to be ſure that they were pores, much leſs what Figure they were of: But judging from the lightneſs and yielding quality of the Cork, that certainly the texture could not be ſo

curious,

MICROGRAPHIA. 113

curious, but that poſſibly, if I could uſe ſome further diligence, I might find it to be diſcernable with a *Microſcope*, I with the ſame ſharp Pen-knife, cut off from the former ſmooth ſurface an exceeding thin piece of it, and placing it on a black object Plate, becauſe it was it ſelf a white body, and caſting the light on it with a deep *plano-convex Glaſs*, I could exceeding plainly perceive it to be all perforated and porous, much like a Hony-comb, but that the pores of it were not regular; yet it was not unlike a Hony-comb in theſe particulars.

Firſt, in that it had a very little ſolid ſubſtance, in compariſon of the empty cavity that was contain'd between, as does more manifeſtly appear by the Figure A and B of the XI. *Scheme*, for the *Interſtitia*, or walls (as I may ſo call them) or partitions of thoſe pores were neer as thin in proportion to their pores, as thoſe thin films of Wax in a Hony-comb (which encloſe and conſtitute the *ſexangular cells*) are to theirs.

Next, in that theſe pores, or cells, were not very deep, but conſiſted of a great many little Boxes, ſeparated out of one continued long pore, by certain *Diaphragms*, as is viſible by the Figure B, which repreſents a ſight of thoſe pores ſplit the long-ways.

I no ſooner diſcern'd theſe (which were indeed the firſt *microſcopical* pores I ever ſaw, and perhaps, that were ever ſeen, for I had not met with any Writer or Perſon, that had made any mention of them before this) but me thought I had with the diſcovery of them, preſently hinted to me the true and intelligible reaſon of all the *Phenomena* of Cork; As,

Firſt, if I enquir'd why it was ſo exceeding light a body? my *Microſcope* could preſently inform me that here was the ſame reaſon evident that there is found for the lightneſs of froth, an empty Hony-comb, Wool, a Spunge, a Pumice-ſtone, or the like; namely, a very ſmall quantity of a

FIG. 32.—Facsimile reproduction of part of the text of Hooke's *Micrographia* in which he describes his observations of the cellular structure of cork.

Discovery of the Nucleus and of Protoplasm.—Robert Brown in 1831 first recognized the importance of the nucleus and its constant occurrence in living cells. He is generally given the credit for its discovery.

The protoplasm of the cell was seen as early as 1772 by Corti. Dujardin, in 1835, noted the constant occurrence, in the cells of certain simple animals, of a jelly-like substance for which he proposed the name, **sarcode,** and which he recognized as the living material of these animals. Eleven years later the botanist von Mohl proposed the name protoplasm for a substance which he found in the cells of plants. In 1861 Max Schultze showed by his studies that a substance such as Dujardin had observed in simple animals was also present in the cells of higher animals, and established the close correspondence in the behavior of the living substance of plants and animals. He formulated what is now generally known as the **Protoplasm Doctrine,** e.g., that the units of organization of living things consist of little masses of protoplasm

surrounding a nucleus and that the protoplasm of plants and that of animals are not essentially different.

Since the appearance of the Protoplasm Doctrine, our knowledge of plant anatomy and cytology has increased enormously. To recount here even the most outstanding discoveries which have been made in

FIG. 33.—Matthias Jakob Schleiden (1804–1881) the German botanist who together with the zoologist, Schwann, propounded *The Cell Theory*. (After Locy.)

this period would make too large a demand upon our space. Among those who have contributed during the past fifty years to the great store of information about the structure and functions of the cell, one of the most outstanding figures is that of Strasburger, for many years Professor of Botany at the University of Bonn. He is famous, not only on account of his many and important discoveries relative to the structure

and behavior of the nucleus and other cell organs, but also because he taught and inspired many of the most active students of the plant cell.

THE PHYSIOLOGY OF THE CELL

Most plants are multicellular, that is, are made up of many cells, hundreds, thousands or even millions of them, and the organs in which

FIG. 34.—Theodor Schwann (1810–1882) the German zoologist who was co-author with Schleiden of *The Cell Theory*. (After Locy.)

the processes just mentioned take place are, in most plants, also multicellular. Yet every function which the plant performs is but the expression of the activities of individual cells, and in unicellular (one-celled) plants all of these processes may be carried on within a single protoplast.

In reading the following account of these physiological processes the student may well keep in mind one of the many different species of

green unicellular plants which may be found by microscopic examination of the water of ponds or streams, of moist soil or of the wet surfaces of stones.

Absorption.—*Solution.*—Since it is impossible for substances to enter the plant cell except in solution in water, it is necessary to learn

FIG. 35.—Max Schultze (1825–1874) who has been called "The father of modern biology." He established the close similarity of the living substance of plants and of animals and was author of *The Protoplasm Doctrine.* (After Locy.)

something of the properties of solutions before we can understand the process of absorption.

On page 46 a true solution was defined and the distinction between true solutions and colloidal solutions pointed out. Except where otherwise stated we shall here use the term *solution* to designate a true solution, that is, solution containing no particles larger than molecules. In every solution at least two or more substances

are present. They are spoken of as the *components* of the solution. It is customary to speak of the component which is present in largest quantity as the *solvent* and of the other component or components as the *solute* or *solutes*. That the distinction between solvent and solute, though a convenient one, is an entirely arbitrary one, is clear when we consider a solution consisting of equal volumes of water and alcohol. In such a solution, we may well ask ourselves which would be the solvent. In the case of the solutions from which plants absorb substances the solvent is generally water. It is true that the atmosphere, a solution of several components, all of which are gases, supplies substances, oxygen and carbon dioxide, which are absorbed by plants, but that gases must go into solution in water before they actually enter the cells. All other substances besides carbon dioxide and oxygen are absorbed, in the case of typical seed-bearing plants, ferns, and mosses, from the water solution existing in the soil. In the case of the unicellular green plants, which we have mentioned, and of other algae, all materials are absorbed from the water (of the sea or of streams, lakes or ponds) in which they are submerged. Soil water, sea water and the water of rivers, ponds and lakes are dilute solutions. That is to say, they are solutions in which the number of molecules and ions of solutes is very small.

A great many of the compounds which are soluble in water exist in solution in water not only as molecules but also as parts of molecules which are called *ions*. Thus a crystal of common salt, NaCl, when dissolved in water yields not only NaCl molecules but also Na^+ and Cl^- ions. These sodium ions and chlorine ions are not the same as atoms for, as the plus and minus signs written after the symbols indicate, they are electrically charged, the sodium ion with a unit positive charge and the chlorine ion with a unit negative charge. When the water of the solution is removed by evaporation or boiling, the ions unite again to form salt molecules. In their properties and behavior ions are quite different from the molecules which produce them. Ions may consist of groups of atoms. Thus when caustic potash, KOH, goes into solution in water some of the molecules break up into K^+ ions and OH^- ions. Similarly sulphuric acid (H_2SO_4), in water may give H^+ ions, HSO_4^- ions, SO_4^- ions and some H_2SO_4 molecules in the solution.

Most of the substances which green plants absorb are more or less ionized (broken down into ions) when in solution in water. Many substances, cane sugar, glucose and glycerine, for instance, do not ionize at all. In the case of compounds which do undergo ionization in water the process is more complete the more dilute the solution. Thus in a very concentrated solution of such a compound very few of the molecules of the solute break up into ions, but in a very dilute solution almost all of the molecules are ionized and very few molecules of solute remain. We shall use the expression *dissolved particles* to include both molecules and ions of a solute.

Diffusion.[1]—This is a process which plays a very important part in the life of the plant. If a piece of blue vitriol (copper sulphate) or

[1] What appears to be a very satisfactory explanation of diffusion in liquid solutions and solutions of gases is furnished by the Kinetic Theory. According to this theory molecules of gases or dissolved particles in liquid solutions are in constant and rapid motion. Any such particle moves in a straight line until it strikes another such particle or the wall of the container. In either case it rebounds and again moves in a straight line until it again collides and rebounds. This goes on indefinitely. A moment's consideration will make it clear that such "jostling" of particles will tend to result in a uniform distribution of each kind of particle throughout the volume of solution, and such uniform distribution is what we call diffusion.

some other deeply colored soluble substance be dropped into a glass of water it will gradually go into solution (Fig. 36). For some time, however, the solution will be more deeply colored in the vicinity of the solid fragment, indicating that the dissolved particles of solute are more crowded or nearer together there, than in more distant parts of the solution. In time the whole solution will become uniform in color, indicating that the dissolved particles of the solute have become uniformly distributed among the water molecules.

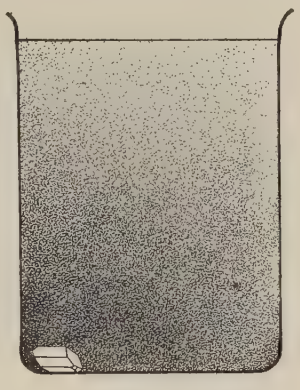


Fig. 36.—Diagrammatic representation of the diffusion of dissolved particles from a crystal undergoing solution in water.

Such scattering of the molecules or ions of one component of a solution among those of the other components, resulting in a uniform distribution of the particles of all components throughout the solution, is called **diffusion.**

Diffusion is not restricted to solutions in water or other liquids but takes place also in solutions in which the components are gases. If even a small quantity of gas of strong and characteristic odor is introduced into the air in one corner of a room, it is soon detectable throughout the room no matter how undisturbed the air has remained. This is due to the diffusion of molecules of the gas throughout the air of the room, the air itself being a solution of oxygen, nitrogen, carbon dioxide and other gases.

Diffusion of solutes in liquids is not a rapid process and when we make a solution we do not ordinarily wait for diffusion to become complete but hasten it by shaking or stirring.

Passage of Solvents Through Membranes.—If water is carefully poured upon a quantity of sugar syrup (a concentrated solution of cane sugar in water) the two fluids will at first form two distinct layers. Soon, however, the molecules of water will diffuse into the concentrated sugar solution and those of the sugar will diffuse into the water, so that finally a uniform solution results. If the syrup and water are separated by a membrane like an ordinary cell wall through which the dissolved particles of sugar and water can pass freely, water will diffuse into the syrup and sugar into the water so that the solutions on the two sides of the membrane will become equal in concentration. Such a membrane which permits water and all solutes to pass freely through it is called a **permeable membrane.**

There are membranes which permit water to pass freely but restrict or prevent the passage of solutes in general or of some solutes at least. Such a membrane is called a **semi-permeable membrane.**

When pure water or a dilute solution of a solute is separated from a concentrated solution by a semi-permeable membrane through which the solute can not pass, an interesting situation results. This will be easier to understand if we think of the membrane as stretched across the U-shaped tube shown in Fig. 37, *A* and *B*.

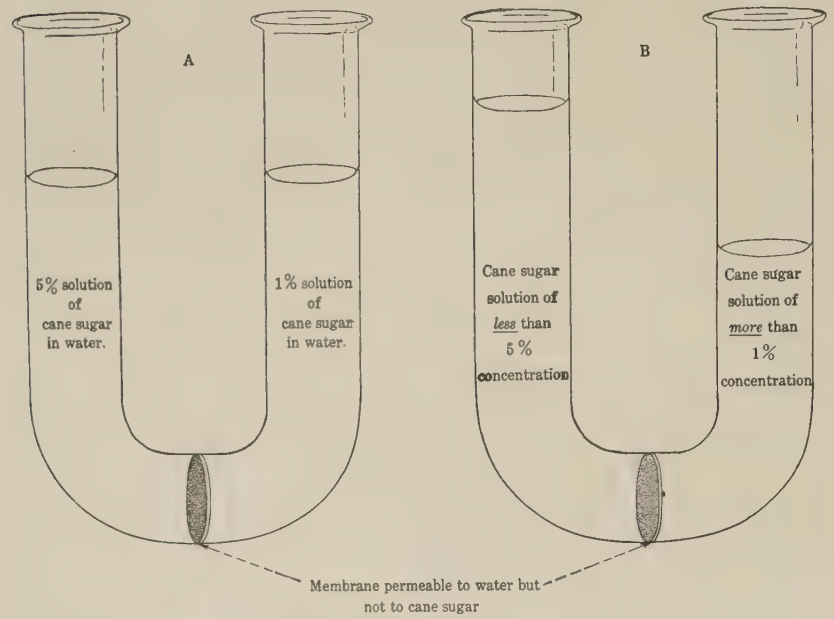


FIG. 37.—Diagram illustrating diffusion through a semi-permeable membrane. For explanation see text.

The left-hand arm of the tube in *A* is partly filled with a solution of 5 grams of **cane sugar** in 100 cubic centimeters of water (what is usually spoken of as a 5 per cent solution).[1] The right-hand arm contains a

[1] Ordinarily when we speak of the concentration of solutions we have in mind the percentage composition, a 1 per cent salt solution being one containing 1 gram of salt in 100 cubic centimeters of water. In this sense it is quite correct to speak of a 1 per cent solution of cane sugar as having the same concentration as a 1 per cent solution of grape sugar or glucose.

It is important to keep in mind, however, that the term concentration, when used in discussions of diffusion and osmosis, refers to the relative *numbers of dissolved particles* of solute (molecules and ions), *not to* the *number of grams*, in a

dilute solution, say 1 per cent, of sugar. The level of the liquids in the two arms of the tube are the same and the two solutions are separated by a membrane which is impermeable to cane sugar. Now water diffuses from the more dilute solution on the right through the membrane to the more concentrated solution on the left.

The solute, cane sugar, tends on the other hand to diffuse from the more concentrated solution on the left of the membrane to the more dilute solution on the right. **The cane sugar will not pass,** however, **because the membrane is not permeable to it.** As a consequence of water passing through the membrane from right to left the following changes occur:

1. The solution in the right arm becomes more concentrated as the result of the loss of water. Its volume becomes less for the same reason.

2. The solution in the left arm becomes more dilute as the result of the addition of water from the other arm. Its volume becomes greater for the same reason.

3. The level of the solutions becomes different, as shown in *B*, the level rising in what was originally the more concentrated solution and falling in what was originally the more dilute.

The difference in level of the solutions in the two arms of the U tube necessitates the conclusion that there is a pressure supporting the column which stands at the higher level. We shall see the existence of the pressure still more clearly demonstrated in what follows.

The passage of the solvent from a quantity of pure solvent or a dilute solution through a semi-permeable membrane into a more concentrated solution is one of the processes which have been included under the term **osmosis** [1] and the pressure of which we have just spoken is called **osmotic pressure.**

The tissue forming the wall of a pig's bladder prevents, or at least greatly hinders, the passage of some solutes through it. That is to say, it is more or less semi-permeable. If such a bladder is filled with a concentrated solution, say of sugar, and the bladder tied shut and immersed in water or a very dilute sugar solution, it soon swells up and becomes stretched and inflated. This condition is the result of water passing

given volume of solution. When concentration is used in this sense it is not correct to speak of a 1 per cent solution of cane sugar as having the same concentration as a 1 per cent solution of grape sugar. A grape-sugar molecule weighs only about one-half as much as a cane-sugar molecule and therefore there are almost twice as many dissolved particles of grape sugar in a cubic centimeter of 1 per cent solution as there are in the same volume of a 1 per cent solution of cane sugar.

[1] The word osmosis has been given such a variety of meanings by those who have used it that it has lost any precise meaning whatever. As far as possible we shall avoid its use.

inward through the semi-permeable wall into the concentrated solution within the bladder. It soon becomes clear that a high osmotic pressure has developed within. This pressure may become sufficient to burst the bladder.

Figure 37 shows still another method of demonstrating this passage of water from a more dilute solution through a semi-permeable membrane into a more concentrated solution. This method also makes it possible to measure the osmotic pressure by determining the height of the column of liquid in the tube.

It should be borne in mind that when two solutions, *A* and *B*, are separated by a membrane the solvent will pass out of solution *A* into solution *B*, thus decreasing the volume of *A* and increasing that of *B*, only if:

1. The membrane is permeable to the solvent.

2. Solutes are present which cannot pass freely through the membrane.

3. The number of dissolved particles of these solutes in a given volume of the solution is greater on one side of the membrane than on the other.

Diffusion of Solutes Through Membranes.—Thus far we have spoken only of the passage of the solvent, generally water, through semi-permeable membranes. However, most semi-permeable membranes permit the dissolved particles of some solutes to pass freely while to those of other solutes they are relatively impermeable. In plants and animals such "selective" membranes are of great importance. We must consider the passage of solutes through membranes. This can best be done by referring to Fig. 38 which is identical with Fig. 37, except for the composition of the solutions in the arms of the U tubes.

The *A* portion of the figure shows a U tube with the right arm filled with a solution of 5 per cent of cane sugar and $\frac{1}{20}$ per cent of common salt and the left arm filled with a solution of 10 per cent cane sugar and $\frac{1}{60}$ per cent solution of common salt. The volumes of the two solutions are the same. The membrane, *M*, separating the two solutions is permeable to water and common salt but not to the cane sugar. The *B* portion of the figure shows the contents of the same U tube some time later. The following changes have taken place:

1. The concentration of salt has become the same on the two sides of the membrane due to salt particles having diffused from the solution where there were more in a given volume ($\frac{1}{20}$ per cent) to the solution where they were fewer ($\frac{1}{60}$ per cent).

2. As in Fig. 37 the concentration of sugar has become the same on

the two sides. This has resulted not from sugar molecules passing through the membrane but from water passing from the more dilute solution (and thus concentrating it) to the more concentrated (and thus diluting it).

3. Osmotic pressure has lifted the level of what was the more concentrated solution above the level of the solution which was at first the less concentrated.

It is the first of these changes which should be emphasized here. As illustrated by Fig. 38 any solute will pass through a semi-permeable membrane from one solution to another provided:

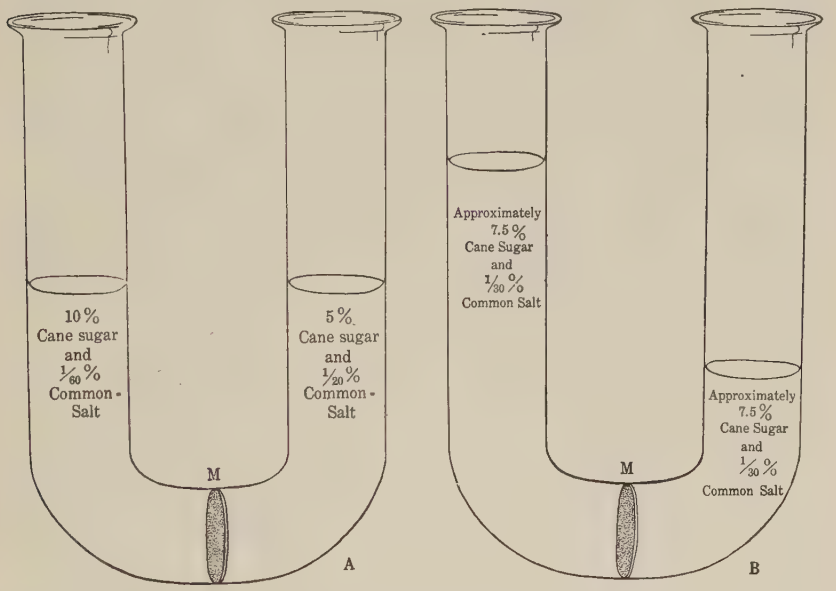


FIG. 38.—Diagram illustrating diffusion through a semi-permeable membrane. For explanation see text.

1. That the membrane, though not permeable to some solutes, is permeable to this particular solute.

2. That this particular solute, present in one of the solutions, is absent from the other solution or present in lower concentration.

3. In general the movement of a particular solute is not affected by the concentrations of other solutes present.

Diffusion in Relation to Absorption by the Plant Cell.—Reference has already been made to certain very simple plants which consist of a single cell floating in water and capable of carrying on all the essential

life functions. We may well use such a cell in pointing out the relation of osmosis to absorption. A cell of this sort is surrounded by a very dilute solution of various solutes (such as carbon dioxide, oxygen and the nitrates, chlorides, sulphates, and phosphates of potassium, sodium, calcium, magnesium, iron and other metals). In the vacuole is the cell sap which is a watery solution with a relatively high concentration of solutes. A large part of the material in solution in the cell sap consists of compounds absorbed out of the surrounding water.

The cellulose wall surrounding the protoplast is a permeable membrane and in most cases can not prevent the passage through it of any of the substances dissolved in the cell sap or in the water surrounding the cell. The cytoplasmic membrane, however, where it is in contact with the cell wall and also where it bounds the vacuole, is semi-permeable. It permits free passage of the water from the outside, and most of the substances dissolved in it. On the other hand, it restricts the passage outward of most of the substances in solution in the cell sap.

Even if we consider the cytoplasmic membranes as semi-permeable we may for simplicity's sake, look upon the two cytoplasmic membranes and the cytoplasm between them as constituting a single membrane. The protoplast may then be compared with a pig's bladder filled with a concentrated sugar solution and immersed in a dilute solution.

The vacuole corresponds with the cavity of the bladder, the cell sap with the concentrated solution within the bladder and the cytoplasm surrounding the vacuole with the wall of the bladder.

In the single plant cell floating in the water, somewhat as in the case of the bladder, water tends to pass from the dilute solution outside into the cell sap. This tends to increase the quantity of cell sap, enlarge the vacuole and create a pressure within the cell.

Added to the pressure resulting from the entrance of water into the vacuole is that resulting from the tendency of the protoplasm to absorb water and swell. This is probably somewhat similar to the imbibition of water by gelatine and other gels.

The pressure within the cell resulting from these two factors (1) absorption of water into the vacuole and (2) imbibition of water by the protoplasm is called **turgor pressure.** The former is very much more important in cells with vacuoles than is the latter.

This pressure would burst the protoplast if it were not for the cell walls. They reinforce or " back up " the protoplast which expands and presses tightly against the cell wall so that the whole cell is distended. The same condition of " inflation " normally exists also in all the many living cells of multicellular (many-celled) plants.

In cells, such as those of the sugar beet, this pressure due to the high

concentration of sugar in the sap in the vacuoles may be as high as 20 kilograms per square centimeter.

When the wall of a living cell has been stretched to a certain extent by the pressure of entering water, the resistance to further stretching just balances the force with which the water passes into the vacuole. Consequently there is no further entrance of water. As we shall show later, every living cell of the plant, even though it be surrounded by other cells instead of being immersed in water, is normally in a condi-

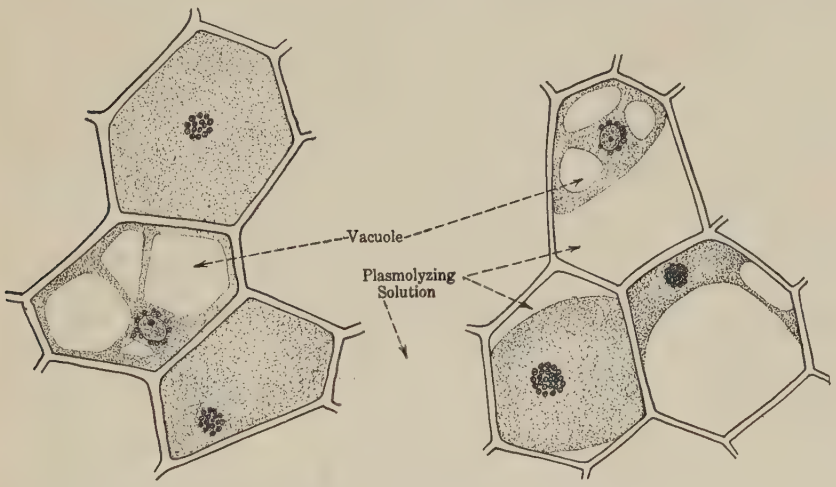


FIG. 39.—Plasmolysis of epidermal cells of wandering Jew (*Zebrina pendula*). *A*, cells in water. *B*, cells after brief immersion in 20 per cent solution of cane sugar. Note that the spaces between the cytoplasm and the cell wall in the plasmolyzed cells are filled with the solution in which the cells are immersed. In each drawing two cells are shown as seen in surface view and one in section.

tion of distension due to turgor pressure. A cell in this condition may be compared to an inflated football. The cell wall corresponds roughly to the leather cover of the football. Although the cell wall is not "solution tight" nor the cover "air tight," the strength of these outer coverings makes it possible for the relatively weak cytoplasmic sac and rubber bladder to withstand high pressure. The stretching of the cover of the football by the pressure of air within the bladder and of the cell wall by turgor pressure within the cytoplasmic sac results in the inflated ball and the turgid cell being plump and firm.

The crispness of the leaves and the rigidity of the young parts of plants is due to the turgid condition of the individual cells. If a turgid cell is placed in a solution more concentrated than its cell sap, water will pass from the cell sap outward through the surrounding cytoplasm

into the solution outside. As a result the vacuole will become smaller, the cytoplasm will shrink away from the cell wall, and the cell will no longer be plump and distended. The cell is then said to be plasmolyzed or to be in a condition of **plasmolysis.** When a crisp lettuce leaf is placed in a solution more concentrated than the cell sap, it wilts as the result of the plasmolysis of the cells of which it is made up. The cell's power to grow in size is largely dependent upon the maintenance of considerable turgor in the cell.

Absorption of Dissolved Substances Into Living Cells.—We have explained how water probably enters the living plant cell and how, as a result, the normal turgid condition of the cell is maintained. But in addition to water the plant must absorb considerable quantities of dissolved substances, such as nitrates, sulphates and phosphates of potassium, calcium and magnesium, the gases, carbon dioxide and oxygen, and various other solutes. As to the method by which the dissolved substances, particularly the inorganic salts, enter plant cells two very different opinions exist among botanists.

The first of these is that the molecules or ions of these substances pass into the cell by simple diffusion, just as salt in the U tube illustrated in Fig. 38, passes from the right arm where the concentration of salt is greater ($\frac{1}{2}$ per cent) through the membrane, which is permeable to it, to the left arm where the concentration of salt is less ($\frac{1}{60}$ per cent). In a water and solute absorbing cell, according to this *simple diffusion theory*, ions and molecules of such a substance as potassium nitrate pass into the cell if the cytoplasm is permeable to them and if such ions or molecules are more concentrated in the solution outside than in the cell sap. If this theory is correct the entrance of dissolved particles of potassium nitrate should cease as soon as their concentration in the cell sap is equal to their concentration in the solution outside.

It is possible to show in many cases, however, that potassium, or calcium or sulphate are accumulated in living cells. Absorption in these cases goes on long after enough has entered to make the concentration inside equal to that outside. This is particularly clearly shown in certain immersed plants growing in the water of ponds or lakes where the concentration of dissolved substances is very low. Those who favor the simple diffusion theory would explain the continued entrance and resulting accumulation of potassium or sulphate or other substances from outside by assuming that the absorbed substances are combined with other materials in the cell into insoluble or indiffusible compounds or otherwise removed from solution in the cell sap.

It has recently been shown, however, that absorbing cells of a

number of plants can continue to take up solutes from dilute solutions even though each of those solutes is actually in solution in the cell sap in many times the concentration it is in the solution outside. There is good reason to think that this may be true of all absorbing cells and it seems impossible to explain this by the simple diffusion theory. Accordingly many botanists are accepting *the theory of active solute absorption.* This theory asserts that living plant cells absorb and accumulate certain solutes by forcing dissolved particles to move from a solution where they are less abundant to the cell sap where they are more abundant.

We may summarize the principal facts pertaining to absorption by the plant cell as follows:

1. All substances which enter a free floating cell or the absorbing cells of multicellular plants must be in true solution in water. This applies to gases as well as other solutes.

2. All substances entering must pass through the cell wall and the cytoplasm before entering the vacuoles. The cell wall is normally saturated with water and permits in most cases everything in true solution to pass. The cytoplasmic membranes are semi-permeable, permitting some solutes to pass through them but not others.

3. Under natural conditions the cell sap is almost always more concentrated than the solution which is present outside the cell, that is, the total number of molecules and ions of solutes of all kinds in a given volume is greater in the cell sap than in the solution outside.

4. Water tends to pass from a less concentrated solution to a more concentrated solution. This means that water molecules tend to pass from a solution where they are more abundant, relative to the number of dissolved particles of all solutes, to a solution where they are less abundant. Therefore they pass generally from outside the cell into the vacuole or vacuoles.

5. The passing of water into the vacuole results in a pressure within the protoplast which might burst the protoplast but for the strength of the cell wall.

6. Imbibition of water by the protoplasm with the attendant swelling of the protoplasm may add somewhat to the pressure within the cell. The total pressure is spoken of as turgor pressure.

7. The cytoplasmic membranes are permeable to some of the many solutes naturally present in the solution outside the cell. Thus some of the substances dissolved in the soil solution outside an absorbing cell may enter the root-hair cell. It may undoubtedly happen that an absorbing cell may at a particular time be (*a*) absorbing water, (*b*) absorbing several different compounds or ions at quite different

rates, (*c*) excluding some solutes, and (*d*) giving out some solute, for example, carbon dioxide.

Photosynthesis.—The green single-celled floating plants to which we have frequently referred in this discussion contain chlorophyll and when illuminated can carry on photosynthesis, the union of water and carbon dioxide to form the sugar, glucose, and starch. The same process goes on in the green cells of multicellular plants.

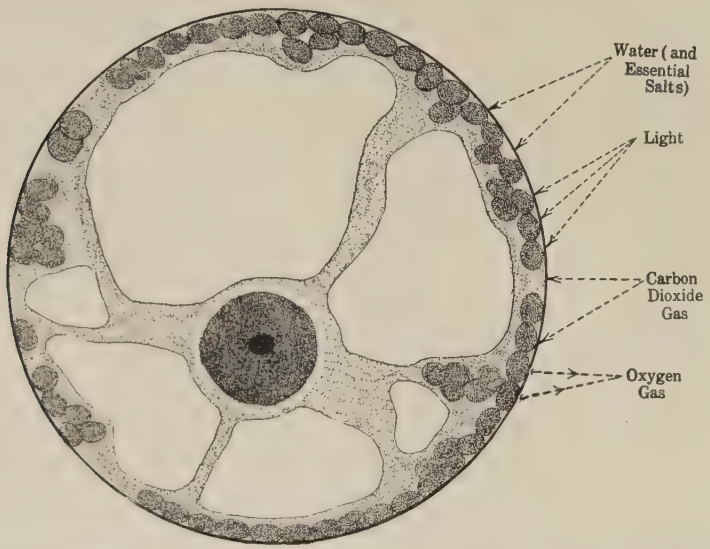


FIG. 40.—Diagram of a unicellular, aquatic plant showing the absorption of materials and energy essential to photosynthesis and the liberation of oxygen which takes place during the process. No attempt has been made to represent the carbohydrate (starch or sugar) produced within the cell by photosynthesis.

The changes which appear to take place in photosynthesis may be briefly stated as follows:

6 molecules of carbon dioxide + 6 molecules of water —(in an illuminated green cell)→ 1 molecule of glucose + 6 molecules of oxygen each consisting of two atoms

When the process is expressed in the form of a chemical equation we get the following as the simplest statement of it:

$$6CO_2 + 6H_2O = C_6H_{12}O_6 + 6O_2.$$

It will be observed that there is more oxygen supplied by the water and carbon dioxide than is necessary for the formation of glucose.

This excess of oxygen is liberated from the plant during photosynthesis.

Photosynthesis is a process which will not go on unless energy is constantly supplied. There are other processes of which we shall learn, which, on the contrary, do not need to be supplied with energy but liberate energy while they are in progress. Light is the source of energy for photosynthesis. This energy is not lost but is stored in the molecule of glucose as **chemical energy**, and can, as we shall see, be recovered and used. It is liberated when the glucose, or related substances which the plant may produce from glucose, are broken down again, in a process called respiration, into carbon dioxide and water.

In the green unicellular plant the sugar produced by photosynthesis may be partly utilized by being converted into the closely related carbohydrate, cellulose, and used to thicken the cell wall. Part of the sugar may be transformed into still another carbohydrate, starch, and held as reserve food in the cell. Fatty substances needed by the protoplast may be produced from the sugar. Proteins may also be built up in such a cell by union of part of the sugar with the nitrogen, sulphur, and phosphorus, derived from inorganic salts. Sugar dissolved in the cell sap of such a cell may be in large part responsible for the high concentration of the sap and therefore for the absorption and retention of water and the maintenance of the turgor of the cell.

During photosynthesis the carbon dioxide used is withdrawn from solution in the water of the vacuole and from the water of the cytoplasm. Thus concentration of dissolved carbon dioxide in the cell sap becomes less than that in the water outside the cell. As a result, diffusion of that gas into the cell goes on as long as active photosynthesis continues.

The liberation of oxygen within the cell by photosynthesis results in that gas becoming more concentrated there than in the water outside. As a result there is outward diffusion of oxygen as long as it is being liberated in the cell.

The process of photosynthesis will be discussed more fully in the chapter on The Leaf.

Respiration.—Another essential process which takes place in the simple, unicellular plant whose functions we are discussing is **respiration.** This process does in fact go on continuously in the protoplasts of all living plant or animal cells. There are constantly going on in the protoplasm activities for which energy is necessary. The only process for which energy from outside the organism can be directly employed is photosynthesis. The energy for all other activities is secured by the respiration of the products of photosynthesis. Thus while photosyn-

thesis is an energy absorbing process, respiration is an energy releasing process and can go on without any supply of energy from outside the plant. In the building up of glucose from carbon dioxide and water, the energy absorbed is stored in the glucose molecule. During respiration the molecules of glucose and related substances are broken down into carbon dioxide and water and stored chemical energy is liberated in forms which can be utilized by the protoplast. Thus it is that all the energy used by plants or animals to carry on their activities is derived, directly or indirectly, from the light of the sun. This energy is stored

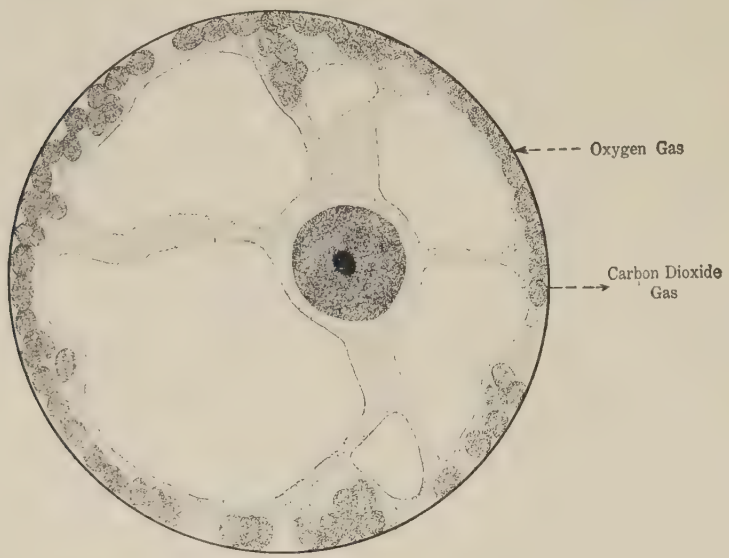


FIG. 41. -Diagram of a unicellular, aquatic plant showing the gas interchange during respiration. In addition to carbon dioxide gas, water is also a product of respiration.

in the food manufactured by photosynthesis, and liberated by respiration.

In many respects respiration and burning are essentially alike. Glucose will burn freely if supplied with sufficient oxygen. The burning of glucose and its respiration in the cells of a living plant or animal have the following similarities: oxygen is necessary for both processes; the substances produced in the two processes are the same, carbon dioxide and water; and in both cases energy is liberated. Both in burning and in respiration the stored chemical energy of the glucose molecule is released. Respiration is clearly different from burning in that it does

not take place outside of living protoplasts and goes on at temperatures much below that necessary for burning.

In man and other warm-blooded animals much of the energy liberated by respiration appears in the form of heat, which is necessary to maintain the normal temperature of the body. A small part of the energy released by this process in plants is also in the form of heat, but it passes off so rapidly to the surrounding atmosphere, soil, or water that plants are seldom appreciably warmer than their surroundings. In the case of the firefly, the glow worm, luminescent bacteria, and certain phosphorescent animals living in the sea, part of the energy of respiration is in the form of light. In all organisms, however, much of the energy liberated by respiration never appears as light or heat but is used directly by the protoplast for the transformation of materials and for other processes which are essential to the life of the cell. In the case of motile organisms (animals or plants which are able to move from place to place) much of the energy derived from respiration is used up in locomotion.

The principal facts relative to respiration and photosynthesis are summarized and contrasted below.

PHOTOSYNTHESIS	RESPIRATION
1. Its raw materials are carbon dioxide and water.	1. Its raw materials are glucose, other foods, and oxygen.
2. It goes on only in cells provided with chlorophyll.	2. It takes place in all living plant or animal cells.
3. It takes place only when the cells are illuminated, therefore, in nature only during the day.	3. It goes on at all times, by night as well as by day.
4. It is an energy absorbing process and continues only so long as light energy is supplied to the cell.	4. It is an energy releasing process and is independent of energy sources outside the plant.
5. The energy absorbed is stored in the sugar molecule.	5. The stored energy of the sugar molecule is liberated in forms useful to the organism, in the plant chiefly as chemical energy.
6. Its products are glucose, or other sugars, and oxygen.	6. When the process goes on to completion its products are carbon dioxide and water.
7. The gas absorbed during photosynthesis is carbon dioxide, and that liberated is oxygen.	7. During respiration oxygen is absorbed and carbon dioxide is liberated.

In a cell like that of the unicellular floating plant to which we have frequently referred, the constructive (**anabolic**) process, photosynthesis, and the destructive (**katabolic**) process, respiration, will go on

simultaneously whenever conditions are favorable for the former. Photosynthesis, while it is taking place, must be more active than respiration, for the only material available for respiration in such a cell is that which has been manufactured in that same cell. If respiration proceeds at as high a rate as the constructive process, death will soon ensue from exhaustion of respirable materials since respiration goes on continuously and photosynthesis only while the cell is illuminated. For a time each day when photosynthesis is slowed down by weak illumination, the two processes, photosynthesis and respiration, may go on at the same rate. During that time there will be no absorption of gas by the cell nor release of gas from it. The oxygen liberated by photosynthesis will be just enough to supply that needed for respiration and the carbon dioxide set free by the latter process will be sufficient to furnish that needed for photosynthesis.

At night, or at other times when glucose manufacture is not in progress, the cell will take in oxygen and give out carbon dioxide. However, when photosynthesis is active the carbon dioxide supplied by respiration will be insufficient for photosynthesis and the oxygen liberated in photosynthesis will be in excess of that needed for respiration. Accordingly the cell will absorb carbon dioxide and give out oxygen.

Assimilation.—The conversion of carbohydrates, fats, and proteins, and simpler nitrogenous foods into the living material (protoplasm) of the cell is called assimilation. It is a process about which we can know very little until we understand much better than at present the nature of the protoplasm itself. This term, assimilation, as used in the sense of transformation of food into protoplasm, must not be confused with the expression, " assimilation of carbon." The latter phrase is used by some botanists to include the absorption of the raw materials for photosynthesis, the formation of sugar, the transfer of sugar from one part of the plant to another, and finally conversion into part of the protoplasm.

It should be explained here that we shall use the term **food** only for those materials which are capable of yielding energy when respired and which may be utilized, without any considerable change, as building material for the protoplasm. For simple substances like water, carbon dioxide, and inorganic salts which the plant can utilize for the manufacture of foods but which can not be respired, we shall use the expression, **raw materials for food manufacture.**

Growth.—In addition to being able to absorb raw materials, to construct foods, to convert these foods into protoplasm, and to secure necessary energy by respiration, the unicellular plant is able to grow. Growth of the cell results in part from the increase in the quantity of

protoplasm, and in part from a stretching of the cell wall due to turgor. During growth sugar is converted into cellulose by the protoplasm lining the cell wall. Thus the thickness of the cell wall may be increased. The growth of a multicellular plant differs from that of a unicellular one; for it involves not only increase in the size of cells and in the quantity of protoplasm but also increase in number of cells.

Multiplication of Cells.—After attaining a certain size the unicellular plant divides into two cells which then separate, and each of which after a period of growth again divides. In multicellular plants this power of repeated division is restricted to certain cells.

Cell division is a process in which there is a definite sequence of complex changes (Fig. 42). First a division of the nucleus into two daughter nuclei takes place. Immediately thereafter, the cytoplasm is divided by a membrane formed between the two daughter nuclei. This is the middle lamella and upon it the two new protoplasts deposit the cellulose, which soon makes up the greater part of the dividing wall. This process of cell division is of such great importance that we are justified in describing it in more detail.

A resting nucleus, that is, one not in a process of division, has already been described. In such a nucleus there is a network of linin, along the strands of which occur here and there chromatin granules (Fig. 42, 1). At the beginning of nuclear division the net takes on the form of a thickened thread which is irregularly coiled. This is called the **spireme** (Fig. 42, 3). Then, the thread splits lengthwise into two strands which remain close together (Fig. 42, 4). Following this, the double thread shortens and breaks up transversely into segments or rod-shaped pieces, each of which still consists of two strands (Fig. 42, 5). These bodies are called **chromosomes.** In all cells of the individuals of a given species, except certain reproductive cells, the number of chromosomes which appear at the time of nuclear division is the same.

While these changes have been going on in the nucleus there arise in the cytoplasm immediately surrounding the nucleus two groups of delicate fibers, which radiate toward the nucleus from two centers, situated on opposite sides of the nucleus. The nuclear membrane then disappears, and the fibers extend to the middle of the nucleus, where some of them become attached to the double chromosomes, and others connect with fibers radiating from the opposite pole, so that there are unbroken threads from pole to pole. At about this stage the nucleolus or nucleoli disappear.

The two cones of fibers meeting near the middle (equator) of the nucleus form the **spindle.**

Now, the double chromosomes become arranged in a plane at the

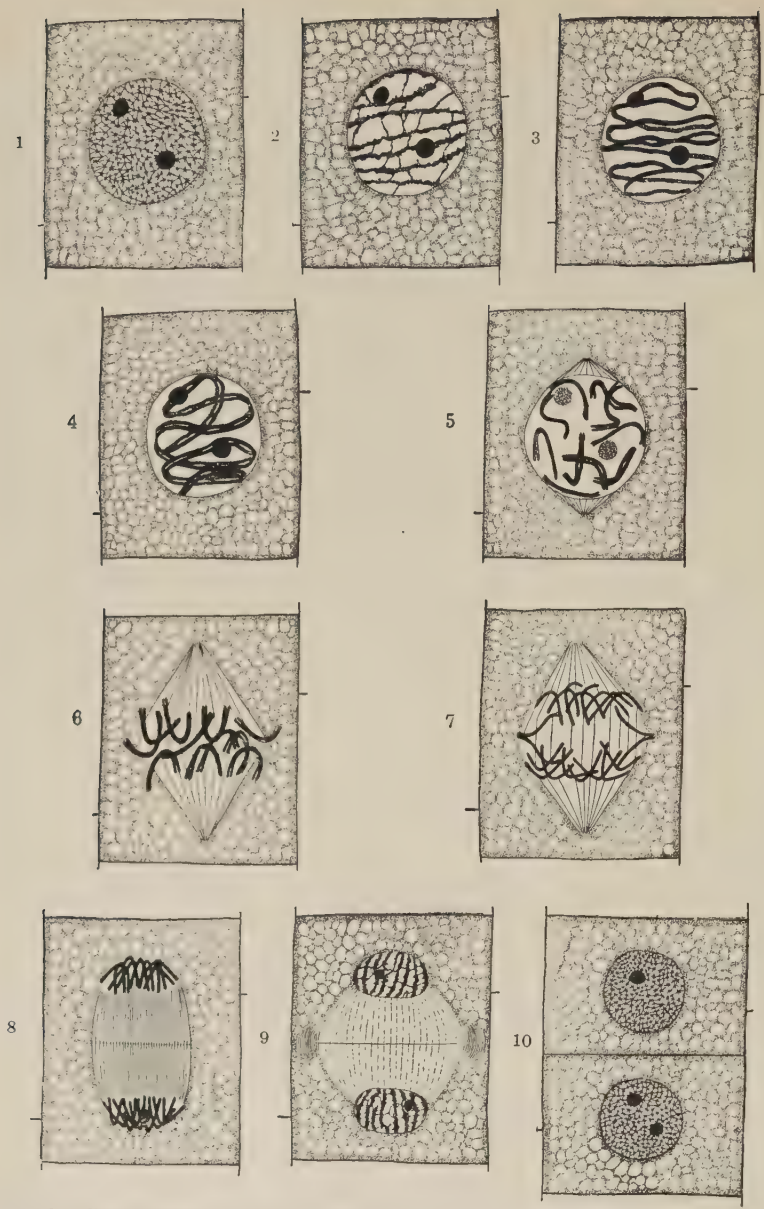


FIG. 42.—Semi-diagrammatic representation of a number of stages in the division of a cell of an onion root-tip. 1, resting nucleus. 2, formation of spireme thread from the nuclear net. 3, the formed spireme thread. 4, longitudinal splitting of the chromatin ribbon. 5, segmentation of the ribbon into chromosomes and beginning of spindle formation. 6, completion of spindle, disappearance of nuclear net and nucleoli, and arrangement of chromosomes at the equator of the spindle. 7, movement of daughter chromosomes toward the poles of the spindle. 8, the daughter chromosomes at the poles of the spindle, the spindle fibers thickening at the equator. 9, the daughter chromosomes reconstructing the nuclear net, reappearance of nucleoli and nuclear membranes, and cell-plate further advanced. 10, daughter cells in resting condition.

equator of the cell (Fig. 42, 6) half way between the two extremities (poles) of the spindle. The halves of the longitudinally split chromosomes, attached to spindle fibers, separate and move towards opposite poles (Fig. 42, 7). Thus there are formed two groups of daughter chromosomes, one at each pole (Fig. 42, 8). Soon, the chromosomes of each group begin to spin out into the form of a nuclear net and thus a daughter nucleus is formed, similar to the parent nucleus (Fig. 42, 9 and 10).

During this reorganization of the two daughter nuclei, the spindle fibers which extend from pole to pole begin to thicken at the equator; then they spread out and come into contact with the lateral walls of the mother cell. Swellings now appear on the thickened fibers at the equator, which increase in size, finally fuse, and thus form a continuous plate (the **cell plate**), which extends across the equator of mother cell and divides it into two daughter cells. The fibers then disappear altogether.

It is customary to divide the entire process of cell division into a number of phases or stages, as follows:

1. *Prophase.*—(Drawings 2–5, Fig. 42.) Formation of the spireme, its contraction, splitting longitudinally, and segmentation into chromosomes (double), accompanied by disappearance of nucleolus and nuclear membrane, and by the beginning of spindle formation.

2. *Metaphase.*—(Drawing 6, Fig. 42.) Arrangement of chromosomes at the equator of the nucleus and their attachment to spindle fibers; completion of spindle.

3. *Anaphase.*—(Drawings 7–8, Fig. 42.) Separation of chromosome halves, their movement toward the poles, and formation of two groups of daughter chromosomes.

4. *Telophase.*—(Drawing 9, Fig. 42.) Reorganization of daughter "resting" nuclei, appearance of nucleolus; construction of cell plate; disappearance of spindle.

It has been previously stated that, in the prophase, the nuclear net first forms a long thread which splits longitudinally, and then transversely, into a definite number of double chromosomes. Whereas this is probably the usual course, in some instances the net forms directly a definite number of chromosomes which are distinct from each other from the first. In either case, however, the longitudinal splitting of the chromosomes is started in the prophase.

It should be added at this point that, following the origin of the cell plate, this structure splits and forms the cytoplasmic membranes of the two daughter cells. Between these two membranes, the daughter protoplasts secrete a material which makes up the middle lamella.

TISSUES

In multicellular plants, particularly those belonging to the Pteridophyta and Spermatophyta, the plant body is made up of many different kinds of cells. Each kind of cell is adapted to serve a certain function in the life of the plant. Cells of similar structure, which together perform a particular function, constitute a **tissue.** The cells of the various tissues may differ in their form, in the thickness of their walls, in the length of life of the protoplast, and in other particulars. We shall here give the characteristics by which cells belonging to the principal tissues may be recognized. In the chapters on the root, leaf, and other organs, these tissues will again come up for discussion, particularly as to their function and their distribution, in the plant. The principal tissues to be discussed here are **meristematic tissue, parenchyma, epidermis, cork, mechanical tissues** and **conducting tissues.**

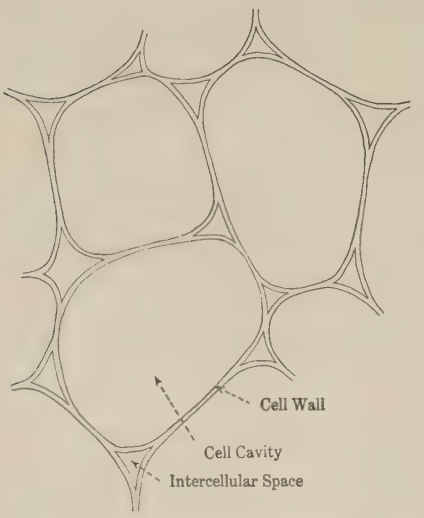


FIG. 43.—Typical parenchyma tissue. The cell contents are not shown.

Meristematic Tissue.—At the tips of all the roots and branches of the plant are groups of cells which by repeated division give rise to new cells. The growth in length of the stem and root results from the formation of these cells and their subsequent elongation. Just outside of the cylinder of wood, which forms the greater part of the stem of a tree or shrub, is a layer, the cells of which by their division continuously add to the wood and to the inner bark. This layer of cells is called a **cambium.** Another cambium produces the outer bark of woody plants. These cambiums and the above-mentioned **growing points** at the tips of roots and stems are called **meristematic tissues.** The cells are thin-walled and seldom much longer than wide. The nucleus makes up a large part of the volume of the protoplast and the vacuoles are either absent or very small. (Fig. 21.) Meristematic tissue is generally compact and without the intercellular spaces (between the cells) which are characteristic of some tissues.

Parenchyma Tissue.—Widely distributed throughout the plant are large isodiametric cells with thin cellulose walls, large vacuoles,

and commonly with air spaces between them (Fig. 43). These air spaces are called intercellular spaces. The protoplasts of these cells

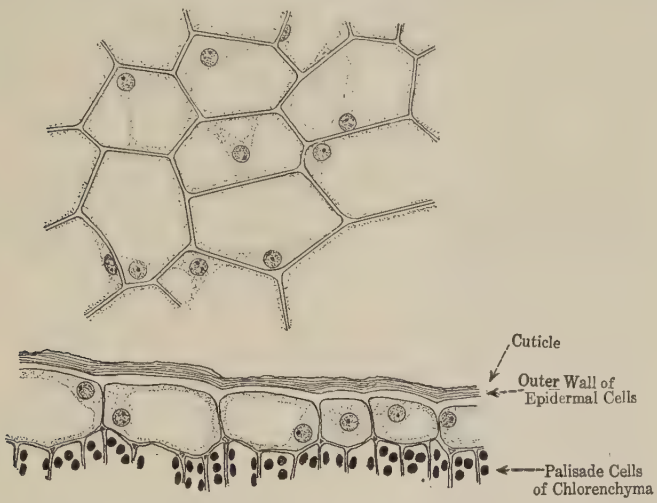


Fig. 44.—Ordinary epidermal cells from the upper side of a leaf. Above, surface view, below, as seen in section. For the stomata and guard cells see Figs. 145 and 146.

remain alive for a long time. Cells of this type constitute a tissue called **parenchyma.** They resemble meristematic cells more closely than do the cells of any other tissue. The green parenchyma of leaves and young stems, which carries on photosynthesis, is often called **chlorenchyma.**

Fig. 45.—Cork cells from the stem of Dutchman's pipe (*Aristolochia*).

Epidermis (Fig. 44).—This is the tissue which forms the surface layer of all parts of ferns and flowering plants that are not covered with bark. Such a layer is found also in some plants below the ferns. Except in the case of a very few plants, the epidermis is one cell thick and on the plant parts above ground consists of cells whose outer walls are thickened and convex and thus fitted to protect underlying tissues from drying out and to some extent from mechanical injury. The protoplasm in epidermal cells forms a thin layer lining the wall. Chloroplasts are generally absent from the epidermal cells except in the case of the

special cells (**guard cells**) which control the small openings (**stomata**) by which gases enter and pass out from the leaves and young stems. The surface layer of the outer epidermal wall of the aerial parts of most plants consists of a waxy substance called **cutin.** This superficial layer, which is called the **cuticle,** covers the entire epidermis of the parts above ground except where the epidermis is replaced by cork. By means of certain

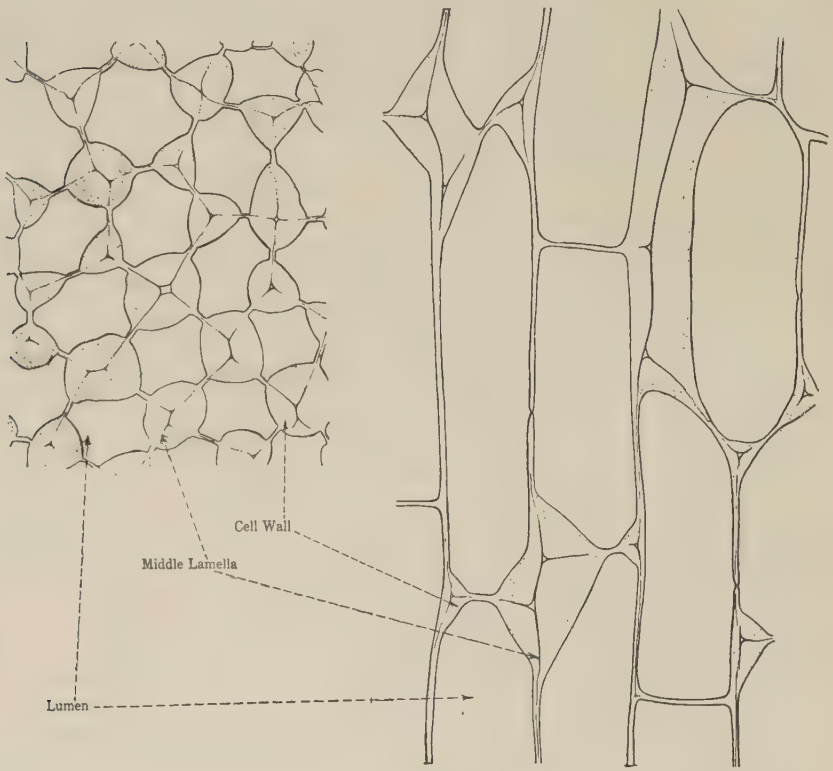


FIG. 46.—Collenchyma tissue. (Left), cross section. (Right), longitudinal section. The cell contents are not shown.

stains and chemical tests it can be easily distinguished from the cellulose of the rest of the cell wall. It is very impermeable to water and gases. The protoplasts of the epidermal cells are long-lived. From the thin-walled epidermal cells of the younger parts of the roots, tubular extensions (root hairs), closed at the ends, grow out into the soil. They are specially fitted to absorb water and inorganic salts from the soil. The structure and function of the root hairs are discussed in more detail on pages 166–169.

Cork.—In the older parts of the stems and of the roots the epidermis is replaced by many layers of a tissue called cork (Fig. 45) which forms the outer bark of trees. It is from this outer bark of the cork oak (*Quercus suber*) that the cork of commerce is secured. The cork cells are generally flattened, and have relatively thin walls and no intercellular spaces. Between the middle lamella and the inner cellulose layer of each of these cells is a layer of a fatty substance, called **suberin,** which renders the cells almost impermeable to water or gases and makes this tissue an excellent protection for the stem against excessive loss of water and against mechanical injury. The protoplasts of cork cells die very soon after the cells are formed.

Mechanical Tissue.—In typical plants a number of different kinds of cells are so differentiated and arranged in the plant body as to give greater mechanical strength than can be secured merely by the high turgidity of the living cells. These cells, which have their walls thickened entirely or in part, constitute the strengthening or mechanical tissues. The principal mechanical tissues are **collenchyma,** fibers of several kinds and **stone cells.**

Collenchyma.—The cells of this tissue are elongated and thickened at the corners. The protoplasts are long-lived and chloroplasts are frequently present. Collenchyma (Fig. 46) is the first of the mechanical tissues to be developed and is found, therefore, even in the young parts of the stem. Its cells are capable of considerable elongation after they are formed. The walls are of pure cellulose.

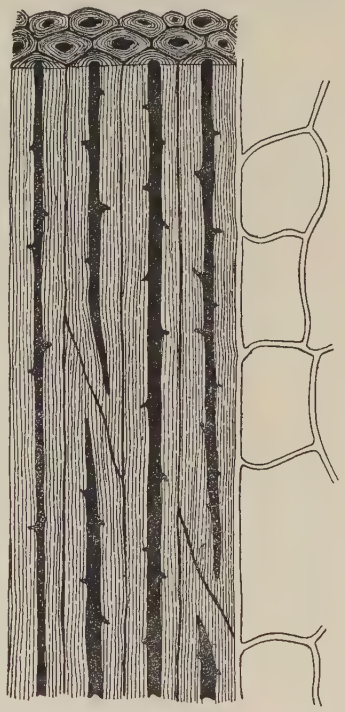


Fig. 47.—Bast fibers and (to the right), several parenchyma cells.

Fibers.—These are elongated cells, thickened all around and generally pointed at the ends (Fig. 47). In extreme cases they may be as long as 10 inches. Soon after the fibers have attained their full size and thickness of walls their protoplasts die. The cell wall of these cells generally undergoes lignification (modification of part of their cellulose into a substance called **lignin**). This change in the cell walls results in an increase in strength and hardness but does not

decrease their permeability to water and dissolved substances. These fibers are very elastic and can be stretched to a remarkable degree without losing their power to return to their original length. They are found in various parts of the plant and are spoken of as wood fibers, cortical fibers, etc., according to their location. They are the most important mechanical elements in the plant.

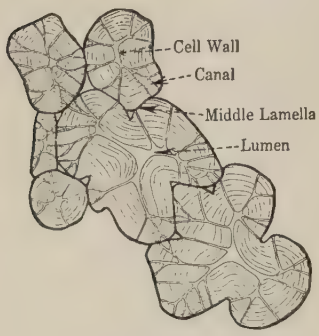


FIG. 48.—Stone cells from the shell of English walnut (*Juglans regia*).

Stone Cells.—These are cells with walls much thickened and lignified like the fibers, but differ from the latter in not being greatly elongated (Fig. 48). From the small cell cavities of these cells minute canals extend outward through the thickened wall. When these cells occur in groups each canal or pit lies opposite to a

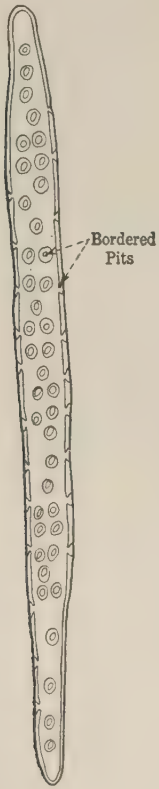


FIG. 49.—A single pitted tracheid from pine (*Pinus*) wood.

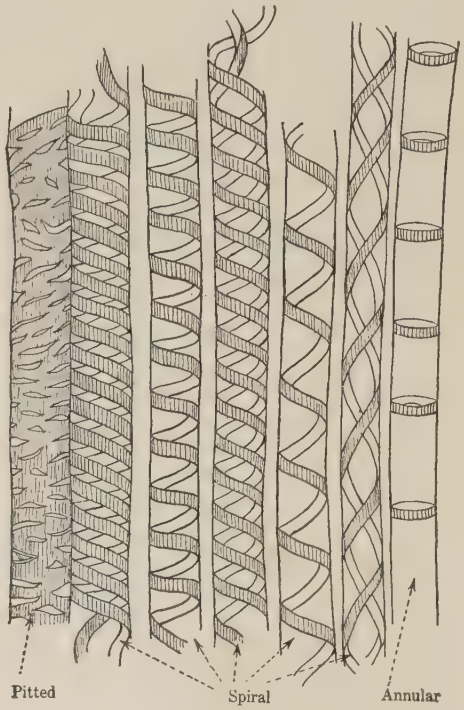


FIG. 50.—Different types of tracheal tubes.

similar pit in an adjoining stone cell, and is separated from it by a thin wall. Thus, passage of material from one cell to another can go on until the thickening is completed and the protoplasts die. Similar pits are often found in the walls of the bast fibers. The gritty texture of the flesh of pears is due to groups of stone cells.

Conducting Tissue.—There are three kinds of structures especially adapted for conduction of materials from one part of the plant to another, **tracheids, tracheal tubes,** and **sieve tubes.**

Tracheids.—These are single dead cells, always elongated, and generally pointed at the ends (Fig. 49). The walls are thin in certain places and thick in others. Sometimes the thickening is restricted to rings or spiral bands running around the cells, in other cases all the wall is thickened except for numerous small, round, or oval areas or pits. The walls of tracheids are always lignified.

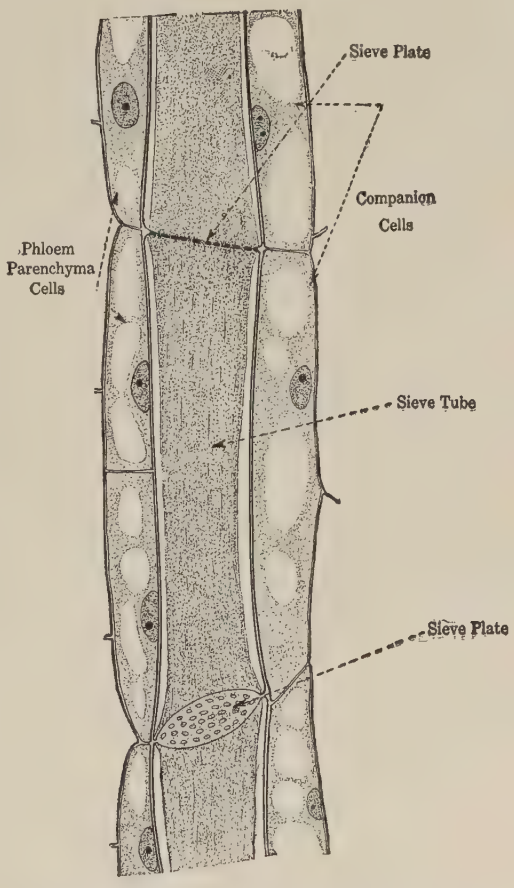


FIG. 51.—A sieve tube and companion cells from the stem of squash (*Cucurbita maxima*).

Tracheal Tubes.—A tracheal tube is not a single cell but is a tube made up of a series of somewhat elongated, cylindrical cells with the end walls dissolved away (Fig. 50). These tubes, like the tracheids, have part of the area of their walls thickened. Those which are formed in a part of the stem which has not yet finished growth in length have thickened rings or spirals. Those which are formed later have the wall much more completely thickened and the thin areas in the form of pits of various shapes. The walls of tracheal tubes, like those of tracheids,

are always lignified. Tracheal tubes are often several centimeters in length (distance between two successive cross walls) and in some trees tracheal tubes exceeding a meter in length occur.

Sieve Tubes.—These are vertical rows of elongated cells with oblique end walls, thickened, and provided with pits (Fig. 51). Through these perforations pass cytoplasmic strands connecting the cytoplasm of adjoining cells.

It was the sieve-like appearance of these end walls that suggested the name sieve tube. The cytoplasm of the sieve tubes is a thin layer surrounding a large central vacuole. In some cases nuclei are lacking from the sieve tubes and soon after the formation of the sieve tube, rows of cells are formed which are equal in length to the cells of which the sieve tubes are made up but smaller in cross section. These contrast strongly with the sieve tubes, not only on account of their smaller size but also because they contain relatively much more cytoplasm. They are called **companion cells.** The walls of these cells and of the sieve tubes are of cellulose. In the walls separating these companion cells from the sieve tubes pits are always present. Proteins and simpler nitrogenous organic compounds are abundant in the sieve tubes, and it is probable that the principal function of the tubes is the conduction of such substances. Proteins, which even in solution pass with difficulty through cell walls, are able to pass freely through the pores of the end walls (**sieve plates**) of these tubes. In many cases a deposit, called **callus,** is formed over the sieve plates and closes the pores. The callus masses are composed of a carbohydrate, **callose.** This stopping of the sieve tubes is permanent in some cases but in others the layer of callus is formed in the late fall and dissolved again in the spring, the sieve tubes then regaining their function of food transfer.

CHAPTER IV

THE STEM

It will be recalled from the account of the Plant Body in an earlier chapter that a typical spermatophyte plant consists of two major divisions, the root and the shoot, and that two kinds of organs make up the shoot, namely, the leaf and the stem. It is the stem which supports the leaves and makes possible such a distribution of them in space that they may freely absorb the essential gases from the atmosphere and receive a large quantity of radiant energy from the sun. The stem also conducts water and soil solutes from the root to the leaves and transports food to different parts of the plant. In addition to these functions the stem, by the activity of the growing points at the tips of the branches, produces more leaves and provides for the growth of the whole shoot. These functions which have been mentioned may be considered to be the primary functions of the stem. Food storage and manufacture of carbohydrates by the green young parts of stems are secondary functions carried on to a certain extent by many stems.

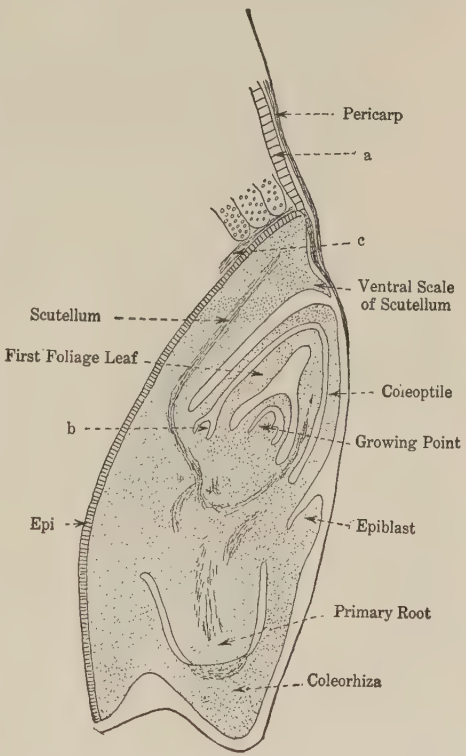


FIG. 52.—Longitudinal section of the embryo of wheat; *a*, aleurone layer; *b*, bud in axil of coleoptile; *c*, crushed empty cells of the endosperm; *Epi*, epithelial layer of the scutellum. (Redrawn from Percival.)

Origin of the Stem.—In the case of most species of Spermatophyta or seed-bearing plants, every individual has had its origin in a seed, although vegetative propagation (development of a new individual from a detached leaf or a piece of root or stem) does occur naturally in a considerable number of species. In every seed there is a rudimentary plant called the embryo, in fact a seed consists merely of such a plant in miniature together with a store of food and protective coats. The embryo plant has at one end a rudimentary root from which the whole root system of the adult plant may develop and at the other a plumule which develops into the shoot. At the center of the plumule is a cone-shaped mass of meristematic tissue which by the division of its cells makes possible the growth of the stem of the seedling plant which generally becomes the main stem of the adult plant. In plants which have developed from seeds, the origin of the stem is then in the terminal bud or plumule of the embryo. In all other cases the stem originates in a bud present upon a stem cutting or developed upon root cuttings or detached leaves. Every branch stem originates also in a bud.

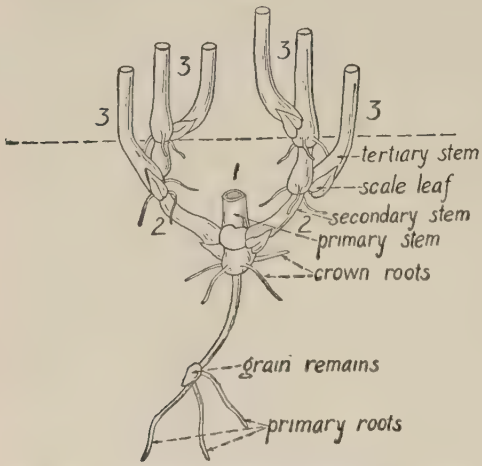


FIG. 53.—Diagram showing tillering in cereals. (From Robbins *Botany of Crop Plants*, after Schindler.)

Growth and Development of Stems.—The growth in length of a stem would not be possible were it not for the addition of new cells at the upper end by divisions of the meristematic cell of the growing point in the terminal bud. Nevertheless it is not at the growing point but some distance behind it that most active elongation of the stem takes place. Passing downward from the very end of the stem, four growth regions or zones may be recognized: (1) a region of meristematic activity with slight growth in length, (2) a region of active elongation, (3) a region of differentiation of tissues in which there is little elongation, and (4) a mature region making up the rest of the stem in which there is no elongation. The first region includes most of that part of the stem which is within the bud. It is generally several nodes and internodes in length. The region of active elongation extends from the base of the

bud downward through several nodes and internodes. The rapid growth in length in this region results from the relatively short and little vacuolated cells of the first region becoming vacuolated, taking up large quantities of water, and stretching lengthwise as a result of the high turgor. As the lowermost internode and node, with its rudimentary leaf or leaves, grow out from the bud and pass into the zone of active

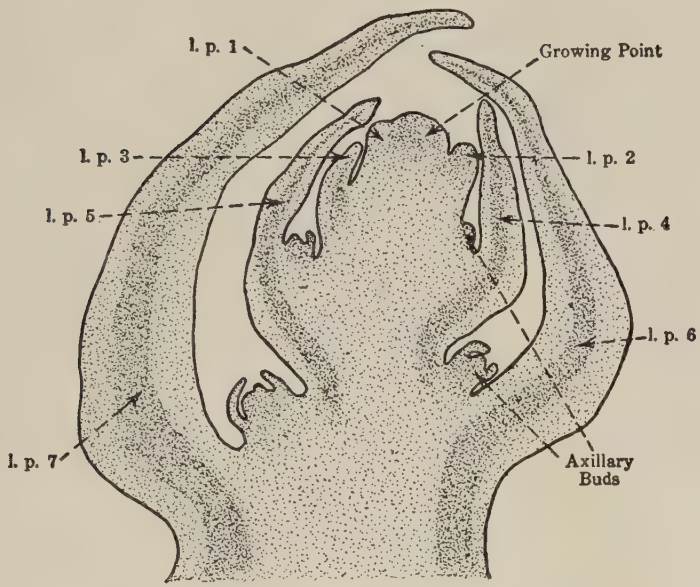


FIG. 54.—Longitudinal section of terminal bud of Dutchman's pipe (*Aristolochia*). The leaf primordia are numbered in the reverse order of their formation, l. p. 1 being the youngest and l. p. 7, the oldest.

elongation, it can be noted that it is principally the internode rather than the node which grows in length. In fact it may be said that most of the increase in length of the stem is due to the elongation of successive internodes. Each internode, at the time this rapid elongation begins, is the lowest internode of the bud, and from that time until its growth stops its length may increase a thousand per cent or even more. The region of differentiation overlaps considerably the region of active elongation for collenchyma and some xylem and phloem elements will be found in portions of the stem which are still increasing in length.

It is generally during and after the rapid elongation of an internode that the rudimentary leaf or leaves of the node immediately below grow into mature leaves.

In most herbaceous plants and in many tropical and subtropical woody plants, growth in stem length continues throughout the whole season of vegetative activity. Thus, during many months successive internodes may elongate, each adding its contribution to the total length of the stem.

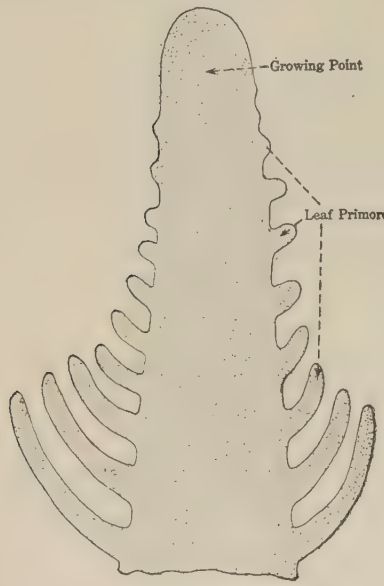


FIG. 55.—A portion of the terminal bud of *Elodea*, an aquatic plant with whorled leaves.

In many woody plants of the temperate and colder regions the elongation in length of the stem is mostly crowded into a few weeks of early spring. This is preceded by swelling of the buds and shedding or separation of the bud scales. Then with a rush of growth the internodes within the buds elongate and the rudimentary leaves unfold and quickly grow to their full size.

STRUCTURE OF STEMS

There are in the stems of different kinds of seed-bearing plants (Spermatophyta) considerable differences in the kinds of tissues present and particularly in the arrangement of the tissues. In discussing the structure and development of stems it is therefore not possible to say much of stems in general. Instead one must choose several types of stems which will illustrate the structure and development of the stems of most Spermatophyta. The principal types of stem structure are (1) the **woody dicotyledon-gymnosperm type,** (2) the **herbaceous dicotyledon type,** and (3) the **monocotyledon type.**

It will be necessary to distinguish here between the principal groups of the Spermatophyta in order that it may be clear of what kinds of plants the different stem types are characteristic. As is shown in the brief outlines of the classification of the Plant Kingdom on page 340 the Spermatophyta are divided into two classes, the Gymnospermae and the Angiospermae. The former, as their name, Gymnospermae

(naked-seeded plants) indicates, bear their seeds, not within a closed structure or fruit as the other seed-bearing plants do, but exposed, generally on the surface of a cone scale. Almost all of the common Gymnospermae have narrow, needle-like or scale-like evergreen leaves, and bear cones. Some of the commonest plants belonging to this class are: the pines (*Pinus*), spruces (*Picea*), firs (*Abies*), hemlock (*Tsuga*),

FIG. 56.—Three ash (*Fraxinus*) twigs showing the opening of the terminal bud. The bud to the left is swelling but the bud scales have not yet separated. The bud scales of the second bud have separated but as yet the internodes and rudimentary leaves within the bud have grown very little. The picture to the right shows the bud fully opened and leaves and internodes well advanced in development.

redwood and big tree (*Sequoia*) and the so-called Oregon pine (*Pseudotsuga*). Most of the common Gymnospermae are trees with excurrent branching and "soft" wood. The Angiospermae include all the other Spermatophyta. Generally they have broad leaves. As mentioned above, the seeds of the Angiospermae (covered-seeded plants) are produced in closed structures, spoken of botanically as fruits. A pea pod, an acorn, and an apple are examples of such seed-enclosing structures.

The Angiospermae consist of two subclasses, the dicotyledons and the monocotyledons. The first of these includes many more species than the second. The grasses, which include the cereals, the lilies, the palms and the orchids are among the principal families of the monocotyledons. Most other common angiosperms are dicotyledons.

Among the most common of the more than 250 families of dictoyledons are the buttercup family, the mustard family, the rose family, the

FIG. 57.—Five twigs of buckeye (*Aesculus*) showing successive stages in the opening of the terminal bud and in the growth of the internodes and leaves which, in a rudimentary condition, were contained within the bud. All the parts above the dotted line belonged to the terminal bud or were developed within a period of three weeks from a terminal bud like the one shown at the extreme left. The scale at the bottom of the figure is a decimeter scale.

bean family and the sunflower family. A large number of those dicotyledons which live for several years are deciduous, losing their leaves once each year and later producing new leaves. In this respect they are in striking contrast with most gymnosperms which are evergreen. There are, however, a few deciduous gymnosperms and many evergreen dicotyledons. The dicotyledons include most agricultural plants of orchard, field and garden, except the cereals, asparagus and onions, which are monocotyledons. Oaks, beech, maple, ash and other "hardwood" forest trees are also dicotyledons.

In discussing stem structure we shall have to use frequently the

terms transverse, radial and tangential as applied to sections of stems. If we think of a piece of a stem as a cylinder and if we use an imaginary line (the long axis) drawn lengthwise through the middle of this cylinder, we may define the three kinds of sections as follows:

A **transverse** or **cross section** is any section cut at right angles to the long axis of the stem.

A **tangential section** is one cut parallel to the long axis of the stem and at right angles to a radius passing through the center line of the section.

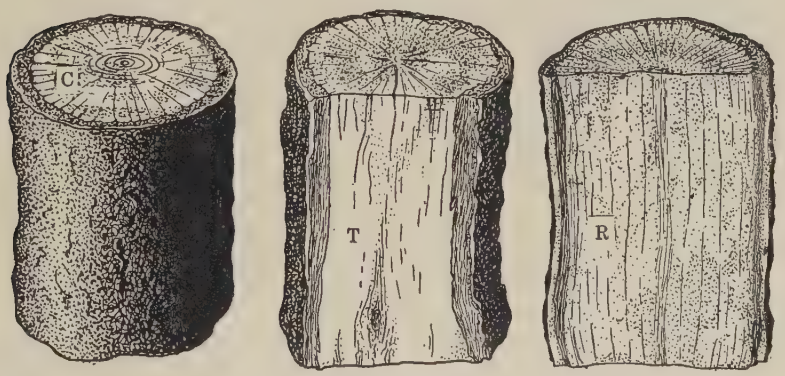


FIG. 58.—Stems showing three kinds of sections: *C*, cross or transverse. *T*, tangential. *R*, radial.

A **radial section** is one cut parallel to the long axis and parallel to the radii passing through it.

Similarly a cell wall may be transverse, tangential or radial. Both radial and tangential sections and cell walls are spoken of as longitudinal.

THE WOODY DICOTYLEDON-GYMNOSPERM TYPE OF STEM

Gross Features of the Structure of Such Stems.—If we examine with the unaided eye or, better, with a pocket lens of low magnification, the cut end of a piece of such a stem, several regions can be made out. If the stem is one to several centimeters in diameter it will be found to consist mostly of a central cylinder of **wood.** The **bark**, which includes the tissues outside of the woody cylinder, may be easily removed, because of the layer of thin-walled, easily broken cells, the **vascular cambium,** lying next to the wood.

Somewhat closer examination of the woody cylinder shows at the center, the **pith,** which consists of softer tissue. It varies greatly in extent in stems of the same diameter but of different species. A number of circular lines concentric with the pith and cambium are present in the wood. The tissue between one of these lines and the next is an **annual ring** and consists of the cells which are added to the wood by the cambium in a single year. The radiating lines of varying length in the wood are the **wood rays.** They are made up of cells fitted for radial conduction of materials in contrast with the longitudinal conduction carried on by the rest of the woody cylinder, and by a portion of the bark. In large stems (see Fig. 73) two regions can often be distinguished in the wood, an inner portion often darker in color and not active in water conduction (the **heartwood**) and the **sapwood** which lies between the heart wood and the cambium.

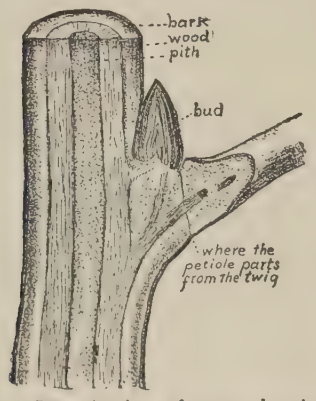


FIG. 59.—Section of stem showing the base of a leaf which is about to fall; also bark, wood and pith as in cross and longitudinal sections. (From Longyear, after Robbins, in *Botany of Crop Plants.*)

Two layers can often be distinguished in the bark, (1) the outer bark generally brownish in color, and corky in character and (2) the inner bark, which in young stems is generally green, just beneath the outer bark and is lighter in color next the cambium.

All of these parts which can be seen on the cut end of a stem (corresponding to the surface of a transverse section) may, with the exception of the wood rays, also be clearly made out on the surface of a stem split along a radius which corresponds to the surface of a radial section. All these features of the woody stem will be discussed in more detail later.

The Origin and Development of the Tissues.—The development of the tissues and the structure of the stem at various ages can best be understood by examining a series of cross sections through the stem from the growing point downward. It should be constantly borne in mind that the greater the distance from the growing point the older the stem region.

The Stem at the Growing Point.—The meristematic cells of the growing point make up a tissue known as the **promeristem.** As already stated (page 80), meristematic cells are essentially alike. They are

small cells without intercellular spaces and having thin cellulose walls, relatively large nuclei, and dense cytoplasm; they are without vacuoles; and they have the capacity for repeated division.

The Stem a Short Distance Back of the Growing Point (Fig. 60).—Just back of the growing point, we note that the cells of the promeristem have differentiated somewhat in size and shape to form three main tissue groups: the **protoderm,** the **ground meristem,** and the **procambium strands.** These three are **primary meristems.** They continue to divide though less actively than the promeristem. By further differentiation they give rise to the **primary permanent tissues** which are tissues no longer capable of active cell division but fitted to carry on the various activities of the stem.

The protoderm is the outermost layer of cells. It develops into the **epidermis,** a primary permanent tissue. When protoderm cells divide, the walls formed are usually radial, that is, at right angles to the surface of the stem. As a result of these radial divisions the protoderm increases in circumference and thus keeps pace with the increasing volume of the underlying tissues.

The ground meristem makes up the greater part of the tissue within the protoderm. It consists of relatively large thin-walled isodiametric cells, among which there may be intercellular spaces. It differentiates into the following primary permanent tissue groups: the **cortex,** and **pericycle,** the **pith rays,** if these are present, and the **pith.**

When procambium cells first become distinguishable from the promeristem they are generally in strands, appearing therefore in a transverse section as isolated groups of cells. These strands are arranged in a circle. A little later more procambium cells may be formed between these strands until in many stems there is produced a continuous hollow cylinder (a ring in section) of procambium. In some stems the strands never join in this way. The procambium cells are smaller, as seen in cross section, than are those of the ground meristem. They are, however, much longer and many of them are pointed at the ends. From the procambium three tissue groups or regions are derived as differentiation goes on. These are the **phloem,** the **cambium** and the **xylem.** In the cases where the procambium strands do not join to form a procambium cylinder, the phloem, xylem and cambium from a single strand constitute a **vascular bundle** and the **cambium** is spoken of as **fascicular cambium** (cambium belonging to a bundle).

The One-year-old Stem.—During the first season's growth of the stem, differentiation of the primary permanent tissues from the primary meristems is completed. These primary permanent tissues consist of the following tissue groups: (1) The epidermis, (2) the primary cortex

and (3) the stele including (*a*) the pericycle, (*b*) the vascular tissue, (*c*) the pith rays if they be present, and (*d*) the pith or medulla.

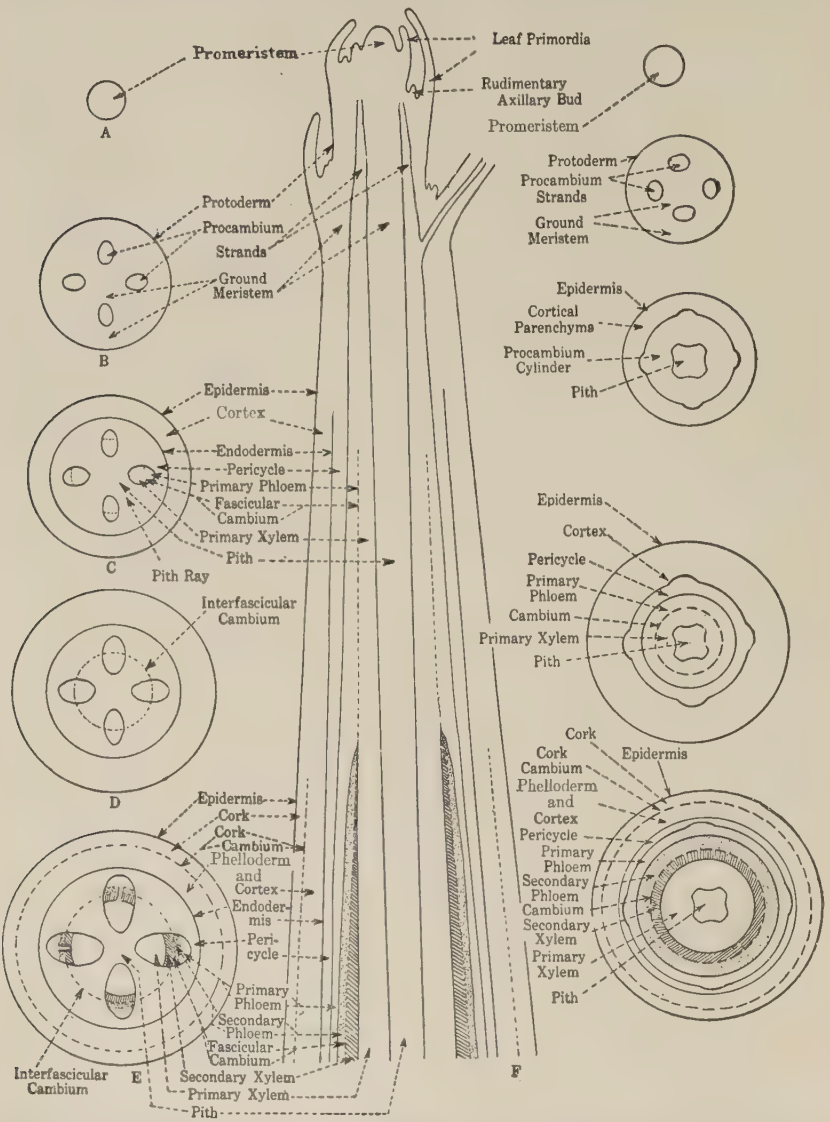


FIG. 60.—Diagram of longitudinal and cross sections of typical dicotyledonous stems; showing primary and secondary growth. Right, cross sections of stem (siponostele); left, cross sections of stem dictyostele).

The Epidermis.—This is usually a single layer of cells generally isodiametric as seen in transverse section but somewhat elongated in

the direction of the stem's length. It will be recalled from the description of the epidermis in an earlier chapter (page 81) that its principal function is the protection of the parts of the plant above ground from excessive water loss, from mechanical injury and from attacks of insects and fungi.

The differentiation which takes place as the protoderm cells change over into epidermal cells consists principally of a thickening of the outer walls and to some extent of the radial walls, whereas the inner

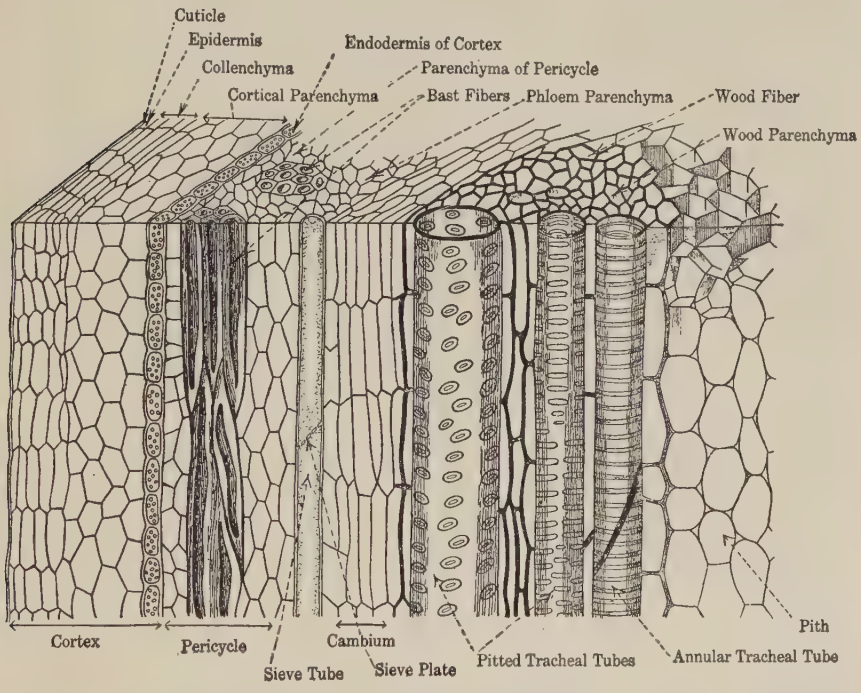


FIG. 61.—Diagram showing portion of dicotyledonous stem in cross and longitudinal sections. (Redrawn from Kerner.)

walls remain thin. While this thickening is going on, the cuticle is being formed and the cellulose wall underneath this layer is sometimes infiltrated with cutin. Some of the protoderm cells undergo the changes which transform them into the guard cells of the stomata.

The Primary Cortex.—The primary cortex, it will be recalled, is one of the regions differentiated from the ground meristem. This tissue group is bounded externally by the epidermis and internally by the pericycle. The primary cortex usually consists of several different kinds of tissue. The outer cells of the cortex, those lying just beneath

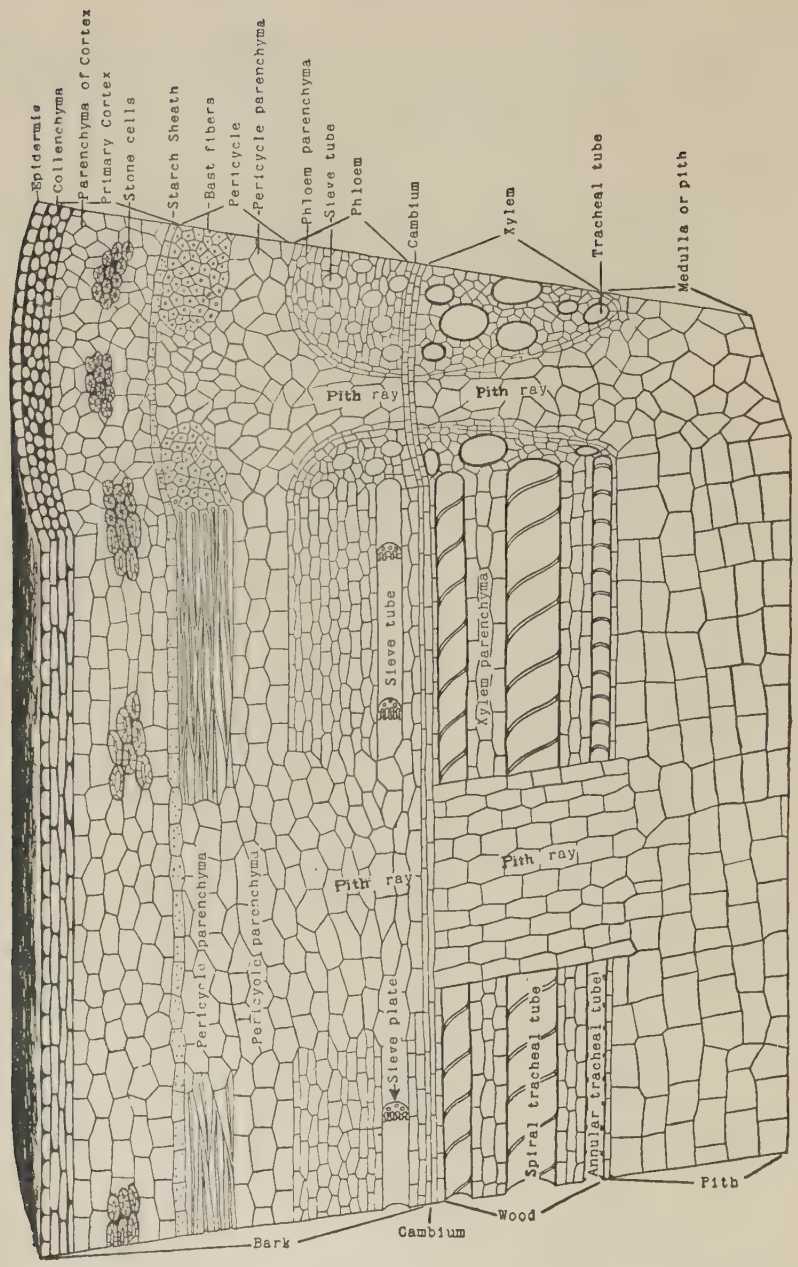


FIG. 62.—Diagram showing the tissues derived from the primary meristems. (After Stevens.)

the epidermis, are usually **collenchyma** which, as has been stated (page 83) constitutes the first mechanical or strengthening tissue of the developing stem.

Beneath the collenchyma is a zone composed chiefly of thin-walled parenchyma which makes up the larger part of the primary cortex. Both the collenchyma and parenchyma cells of the cortex usually pos-

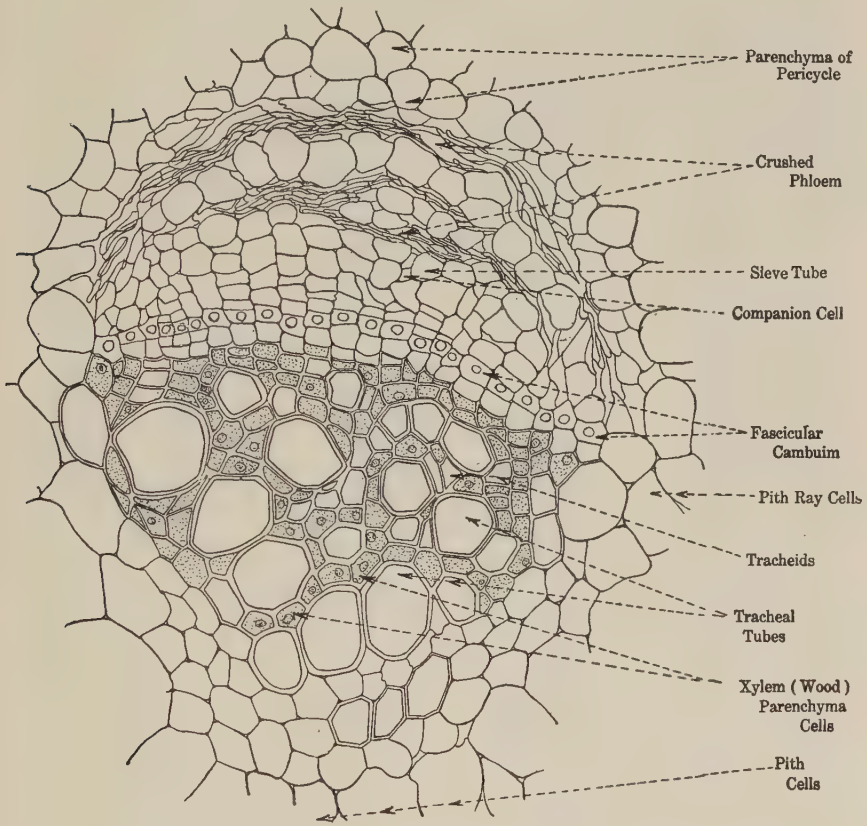


FIG. 63.—Cross section of a young vascular bundle of a dicotyledonous stem. (*Aristolochia.*)

sess chloroplasts and consequently have the power of photosynthesis. In addition to collenchyma and parenchyma, sclerenchyma cells (stone cells or cortical fibers) are also sometimes found in this region. The sclerenchyma cells are lignified.

Not all the cells of the cortex change over simultaneously from ground meristem cells. The same is true indeed of the transformation

of procambium cells into the permanent tissues to which they give rise. The change from ground meristem cells to collenchyma involves lengthening of the cells and thickening of the corners; and the differentiation of the fibers is accompanied by elongation and thickening of the walls "all around." When meristem cells become parenchyma there is less change involved, the cells merely growing in size in all directions, developing at the same time larger vacuoles and intercellular spaces.

The Pericycle.—Within the cortex is the region called the pericycle which extends inward to the phloem. In woody stems it is not sharply marked off from the cortex though in herbaceous stems the innermost cells of the cortex form a single clearly defined layer, the endodermis, the cells of which are recognizable on account of their form and frequently by the presence of starch grains. The pericycle is usually composed of two sorts of tissue, sclerenchyma and parenchyma. The sclerenchyma of the pericycle is made up of closely fitting fibers. These may form isolated groups opposite the vascular bundles or may form a continuous ring. The parenchyma cells of the pericycle may, like those of the cortex, contain chloroplasts and carry on photosynthesis.

The Pith.—This also is formed by the transformation of ground meristem cells. It is made up of large-celled parenchyma with relatively numerous intercellular spaces and its principal function in woody stems is food storage.

Pith Rays.—It was stated above that in some stems the procambium is in the form of a continuous hollow cylinder. This is in fact the case in most stems of the woody dicotyledon-gymnosperm type but there are also many in which the procambium remains in separate strands. In such cases each strand becomes differentiated into a vascular bundle and between these bundles wide strips of parenchyma extend from the pith to the pericycle. Since these strips may well be considered to be extensions of the pith they are spoken of as **pith rays.** They may be distinguished from other rays by the fact that they always extend clear to the pith. They also extend longitudinally from one node through an entire internode to the next node.

The Vascular Tissue.—The procambium cells on the outer side of the strand or cylinder become transformed into phloem and on the inside, into xylem. Only a few of the phloem and xylem elements are differentiated at first but their number increases with the distance from the promeristem. Some of the procambium cells lying between the xylem and phloem do not differentiate but, as a cambium layer, continue to function as meristematic cells.

The Phloem.—The phloem of dicotyledonous stems is made up of three kinds of tissue elements: **sieve tubes, companion cells,** and **phloem parenchyma** cells. Sometimes fibers are also present. An account of the structure of these tissue elements has already been given on page 86. It will be recalled that each sieve tube is a single row of elongated cells placed end to end, and that the thickened end walls of

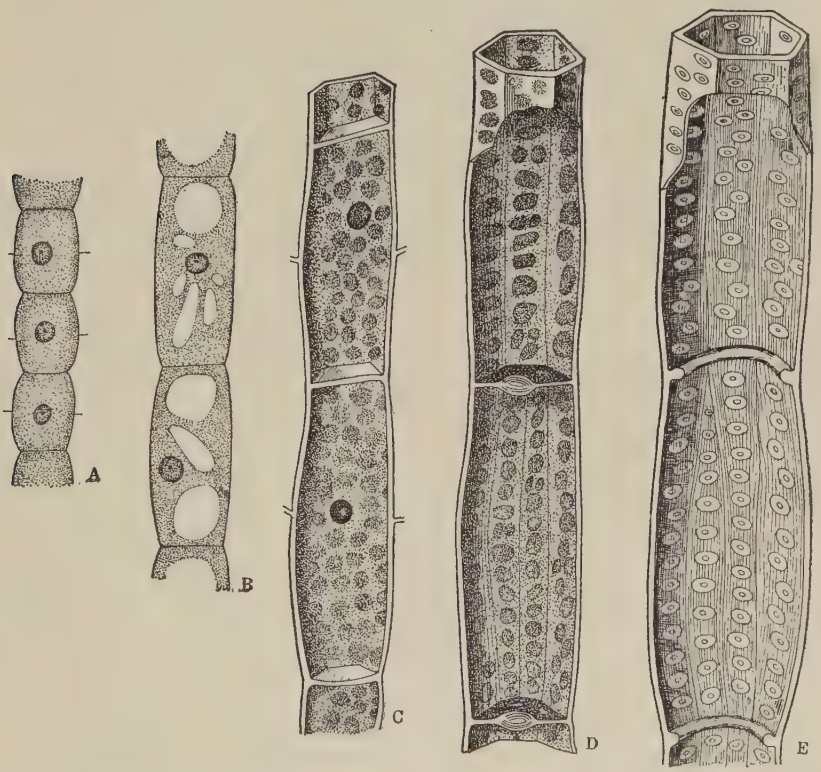


FIG. 64.—Stages in the development of a pitted tracheal tube from procambium strand cells. (After Bonnier and Sablon.)

these cells have numerous perforations. It is on this account that they are called sieve tubes. Through these perforations the protoplasm of each cell of the sieve tube connects with that of adjoining sieve tube cells. Each sieve tube is accompanied by a single parallel row of small cells, the **companion cells.** Among the sieve tubes and companion cells are phloem parenchyma cells which are somewhat elongated vertically, although they do not reach any considerable length. Phloem fibers are also often present.

The phloem of gymnosperm stems is essentially the same as that of woody dicotyledons except that companion cells are not present.

The Cambium.—When most of the cells of the procambium, as mentioned above become differentiated into phloem and xylem and lose their ability to divide, a narrow band of cells between the xylem and phloem remains undifferentiated and retains the power of division, that is, remains meristematic. It is to be considered a primary meristem which persists after the protoderm, ground meristem and most of the procambium have differentiated. This **cambium** is made up of small, thin-walled cells which are flattened tangentially and which are rich in protoplasm, and capable of repeated division.

The cambium layer by its division gives rise to new phloem and xylem and thus causes the stem to increase in thickness. It is often spoken of as a **lateral meristem** in contrast to the **apical meristems** (promeristem, protoderm, ground meristem and procambium) of the growing points.

Xylem (Wood).—The principal structural elements which compose the xylem, or wood, of one-year-old dicotyledonous stems are: **tracheal tubes, tracheids,** and **wood parencyhma.** Tracheal tubes are absent from the wood of most gymnosperms.

Tracheal Tubes (Tracheae).—These are long tubes of considerable diameter, which have been formed by the elongation and enlargement of rows of cells of the procambium strand; in this differentiation of procambial cells, most of the end walls are totally or partially dissolved. Thus, a row of cells becomes transformed into a tube of considerable length closed at either end by walls which were not dissolved. At the time of the formation of the tracheal tube the protoplasm of the component cells dies. Functional tracheal tubes have, therefore, no living contents (Fig. 65). The walls of tracheal tubes become thickened, and the thickening material is laid down on the walls in various patterns, such that thick and thin regions alternate. The material laid down is in the nature of cellulose, but subsequent physical and chemical changes occur, known collectively as **lignification** (impregnation of the cellulose with a substance called **lignin**).

Based upon their sculpturing, that is, upon the distribution of the thinner and thicker area of the cell walls, there are the following kinds of tracheal tubes: **annular, spiral, reticulate,** and **dotted** or **pitted** (Fig. 50). As the name indicates, the thickened areas in the annular (ringed) tube, are of material laid down in the form of rings so that the tube may be compared to a long sack held open here and there by hoops fastened inside it. In the spiral tubes the thickened part of the wall forms a spiral. Annular and spiral vessels are the only kinds found in

the xylem which is first differentiated from the procambium. The thinness of the wall between the rings or spirals permits these vessels to subsequently elongate as the portion of the stem in which they originate grows in length. In reticulate tracheae the strengthening material is deposited in such a fashion as to form a network pattern on the wall. In dotted or pitted tracheae the mode of thickening is such as to leave

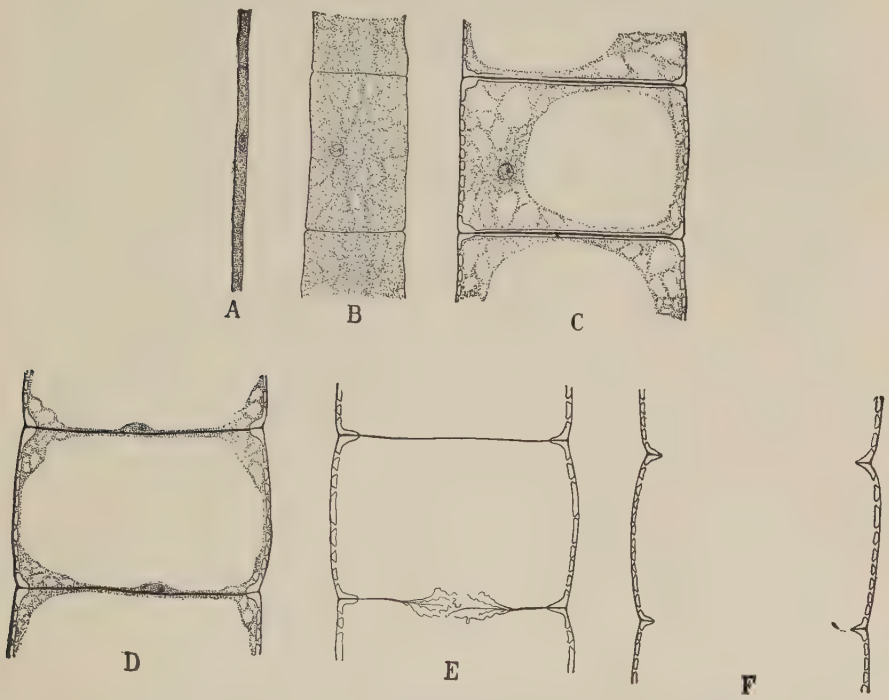


FIG. 65.—Development of the vessel segment in *Robinia pseudo-acacia*. *A*, the cambium initial. *B*, the cell much enlarged. *C*, the cell still further enlarged, the secondary wall well developed. *D*, the cytoplasm restricted to the periphery, the nucleus adjacent to the wall where dissolution is occurring. *E*, the cytoplasm lost, the very thin end walls disintegrating. *F*, the mature, perforated empty cell. (From Eames and MacDaniels, *An Introduction to Plant Anatomy*, McGraw-Hill Book Co.)

numerous circular thin places in the wall which give it a dotted or pitted appearance. Tracheal tubes are the chief conductors of water and mineral salts from the soil to and throughout the leaves in all vascular plants except gymnosperms, in which tracheids are the principal xylem elements.

Tracheids.—In contrast with tracheal tubes, the tracheids are single elongated cells more or less pointed at the ends. Their length

seldom exceeds 1 millimeter and they have thick lignified walls which are in most cases pitted. There are also spiral and annular (ringed) tracheids. In pitted tracheids both simple and bordered pits may occur.

In simple (unbordered) pits, which also occur in tracheal tubes and vascular ray cells, the pit cavity is about the same width throughout. In **bordered pits,** however, which are best exemplified in the tracheids of conifers (Fig. 66), the thickened portion of the wall overarches the margins of the pit. Sometimes the original cell wall or closing membrane of the pit has a thickened area called the **torus.** The thinner marginal part of the closing membrane may be perforated by numerous, small openings. The tracheids, like the tracheal tubes, carry water and inorganic salts. They also are important in giving strength to the woody stem. Like tracheal tubes, tracheids probably do not function to any extent in conduction until their protoplasts die. It seems likely that the thin areas in the walls of tracheal tubes and tracheids make conduction of sap from one conducting element to another easier. The thick areas may, on the other hand, prevent the collapse of the walls (and resultant blocking of the cavities) when sap is being drawn up the stem by suction from above.

Fig. 66.—Diagram showing the the structure of a bordered pit. Above, the pit is shown in section.

Wood Parenchyma Cells.—These are short, thin-walled cells which may have simple pits. Their protoplasts remain alive for a long time, surviving long after those of the tubes, tracheids and wood fibers are dead. They are found here and there among the other elements of the xylem. Their function is the storage of water and food, and they also conduct these substances for short distances.

A Summary of Primary Permanent Tissues.—In our study of the young woody dicotyledonous stem we have been concerned only with the tissues derived from the primary meristems. At the growing point of the stem there is just one tissue—the promeristem. This meristem gives rise to three primary meristems: **protoderm, ground meristem,** and **procambium strands.**

These tissues further differentiate into the **primary permanent tissues.** In the following outline, the primary permanent tissues of the dicotyledonous stem are enumerated and the origin of each indicated.

1. Promeristem	2. Primary Meristems:	3. Primary Permanent Tissues			
	Protoderm	Epidermis			
	Ground meristem	Cortex	Collenchyma		
			Parenchyma		
			Endodermis		
		Pericycle	Sclerenchyma		
			Parenchyma		
		(Pith rays when present).			
		Pith			
	Procambium	Primary phloem	Phloem parenchyma	Vascular Tissue	Stele
			Sieve tubes		
			Companion cells		
			Phloem fibers		
		Fascicular cambium			
		Primary xylem	Tracheal tubes		
			Tracheids		
			Wood fibers		
	Vascular cambium		Wood parenchyma		

Differences in Primary Permanent Tissues of Woody Gymnosperm.—*Dicotyledon Stems.*—Not all the tissues listed in the right-hand column of the summary are present among the primary tissues of all stems of the type we are discussing. Thus tracheal tubes are absent from the xylem and companion cells from the phloem of the gymnosperms, and in some dicotyledons, tracheids are not found among the primary tissues.

The Stele.—To the pericycle and the tissues which it encloses, whether in stem or root the collective term, **stele**, is frequently applied. If this term is used, one may speak of the primary permanent tissues as making up the epidermis, cortex and stele. When the phloem and xylem (vascular tissue) form a continuous hollow cylinder with pith in the center the stele is called a **siphonostele,** and this is the type of stele found in most woody gymnosperm-dicotyledon stems. When the vascular tissue occurs in a ring of vascular bundles surrounding the pith and separated from each other by pith rays, the stele is spoken of as a **dictyostele.** This type of stele is found in the stem of *Aristolochia*, *Platanus* (the sycamore), and other woody stems.

Secondary Growth in the Woody Dicotyledon-Gymnosperm Stem.—The changes from promeristem to the primary permanent tissues given in the summary above are spoken of as the primary growth of the stem. This phase of the stem's development ends when all the tissues have differentiated except the cambium, which remains meristematic throughout the life of the stem. By the time the primary growth has been completed the part of the stem in question has generally finished elongation. Normally this primary growth is completed within a few months. Following this there is a secondary growth which may continue for hundreds of years, or even several thousands in the sequoias. This is attended by increase in thickness. Secondary growth results from

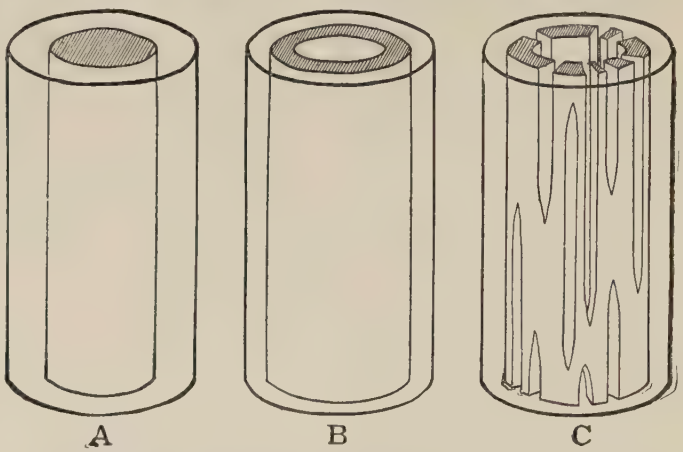


Fig. 67.—Diagram illustrating the types of arrangement of vascular tissues in steles. *A*, protostele; *B*, siphonostele; *C*, dictyostele. (From Eames and MacDaniels, *An Introduction to Plant Anatomy*, McGraw-Hill Book Co.)

the production of new cells by two lateral meristems, the **vascular cambium,** which has already been mentioned and the **phellogen**, or cork cambium.

The Cambium Ring.—In stems with the vascular tissue in a continuous cylinder (stems with siphonosteles) the vascular cambium is at this time already in the form of a continuous ring.

In those having separate vascular bundles (stems with dictyosteles) the cambium is interrupted by the pith rays. In such cases, certain pith-ray cells lying between the cambium of adjoining bundles undergo cell division, giving rise to a row of rectangular meristematic cells similar to those of the bundle cambium, and known as **interfascicular cambium** (Fig. 68). Thus there is formed in these stems also a **continuous vascular cambium ring.**

The cambium ring generally consists of a single layer of meristematcells, which by their repeated tangential divisions, give rise to new xylem and phloem elements (Fig. 69). When a new xylem element is to be formed, a cambium cell divides into two daughter cells, by a tangential wall. As a rule the inner daughter cell, which is the one next to the xylem, develops into a xylem element and the outer daughter cell, next to the phloem, remains a cambium cell. Then this cell, which has remained cambium, again divides and, as before, the outer daughter cell retains its power of division. Less frequently, when a

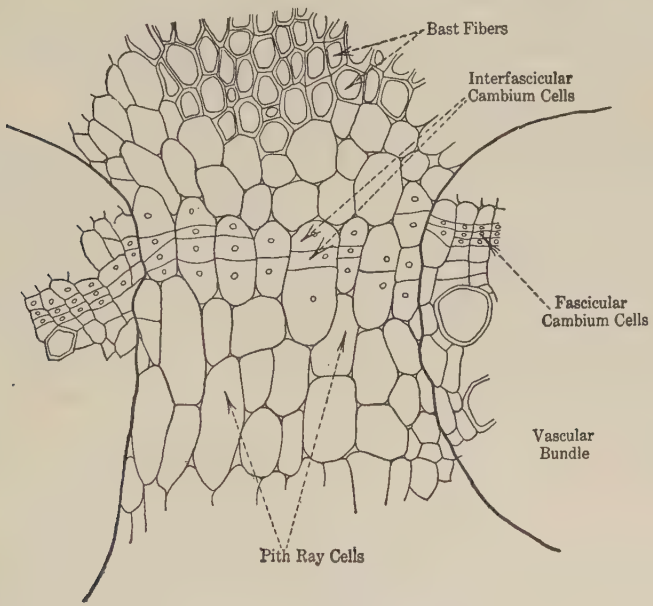


FIG. 68.—Part of a pith ray and two vascular bundles of a young Aristolochia stem, showing the origin in the stem of interfascicular cambium cells from pith ray cells.

cambium cell divides into two daughter cells, the outer daughter cell, which is the one next to the phloem, develops into a phloem element and the inner daughter cell remains meristematic. This process is repeated throughout the growing season. Thus by division of these cells of the cambium ring, new xylem is added on the *outside* of the old xylem, and new phloem is added on the *inside* of the previously formed phloem. The tissue elements produced on the xylem side of the cambium may be wood parenchyma cells, tracheal tubes, tracheids and wood fibers. The latter differ from tracheids in having thicker walls

and much-reduced pits and thus are better fitted for strengthening the stem and less fitted for water conduction than are the tracheids.

As the width of the xylem (from vascular cambium to pith) increases, the distance between the phloem and the inner xylem becomes greater. There is presumably, as a result, need for better conduction of water radially from the xylem to the phloem and of food from the phloem to the xylem. This need seems to be met (though no intent or design on the part of the plant is to be implied) by the production of **vascular rays** by the cambium. Here and there a longitudinal row of cambium cells or several adjoining rows cease the production of xylem and phloem and from now on produce parenchymatous cells which are somewhat elongated radially. The resulting bands of parenchymatous tissue

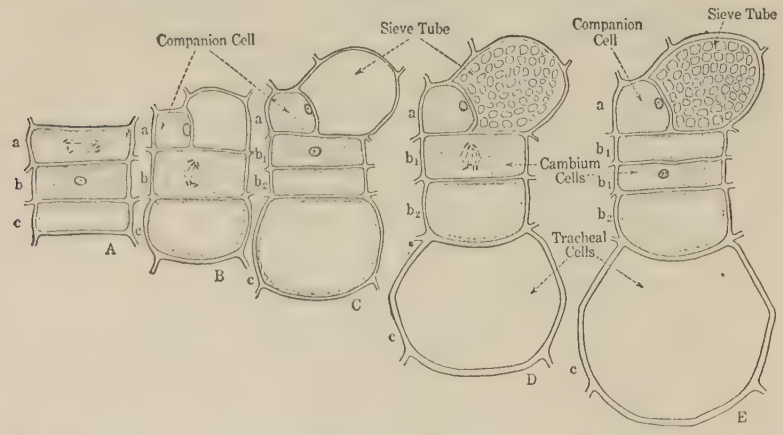


FIG. 69.—Stages showing the differentiation of cambial cells. Diagrammatic.

which seem clearly fitted for transverse conduction of material soon extend into the **secondary phloem** (phloem produced from cambium and not from the procambium direct) and into the **secondary xylem.** On account of their difference of origin they should be carefully distinguished from the pith rays of dictyostele stems. The principal points of distinction beside the difference in origin are: (*a*) pith rays are for a given stem fixed in number; (*b*) they extend from the pith to the pericycle; (*c*) they generally extend longitudinally through an entire internode, from node to node; (*d*) they are primary in origin in that their tissue is formed by the differentiation of the ground meristem, though secondary tissue is added to them by the interfascicular cambium as they elongate radially. Vascular rays, on the other hand, are:

(*a*) not fixed in number for as the stem grows older more and more are produced and (*b*) they never extend inward as far as the pith nor outward

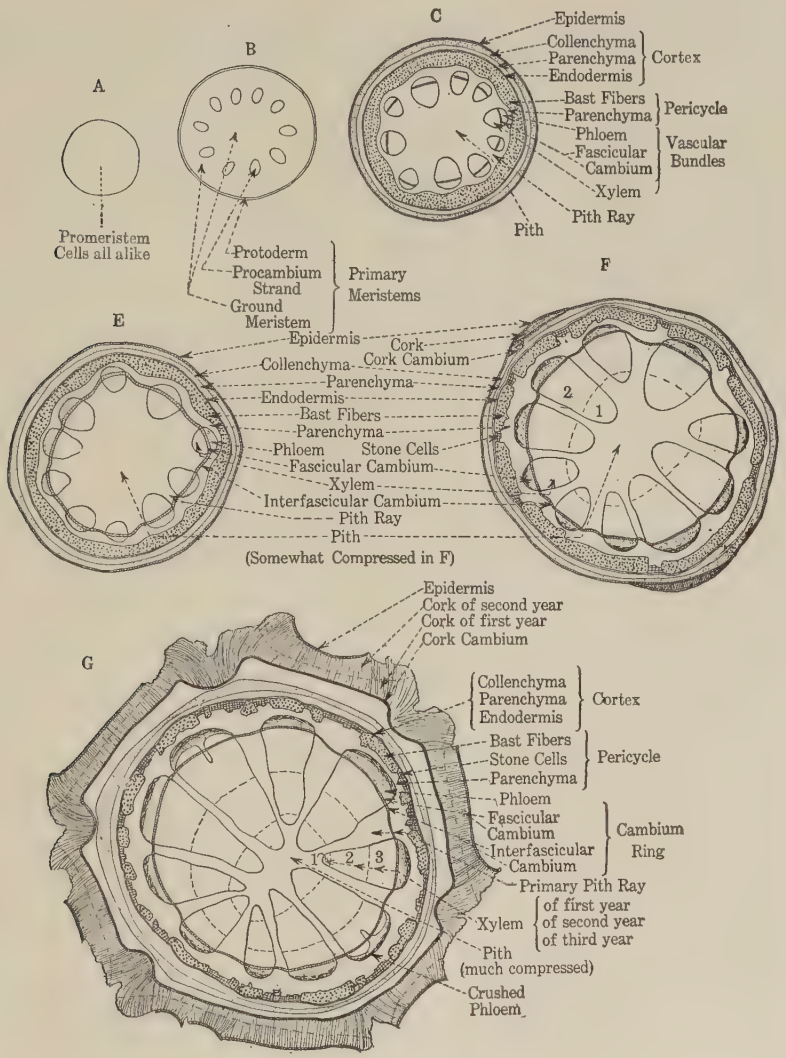


FIG. 70.—Diagrams showing primary and secondary growth of a three-year old dicotyledonous stem (*Aristolochia*) as seen in cross section.

to the pericycle. In a longitudinal direction a vascular ray extends for only a few cells, never throughout the length of an internode.

Finally they are secondary in their origin, arising from the cambium and never from procambium. The part of a vascular ray which is in the xylem is often spoken of as a **xylem** (wood) **ray,** that in the phloem, as a **phloem ray.**

Due to the enlargement of the cylinder of tissue within the cambium ring, as a result of the addition of cells to that cylinder by the cambium itself, it becomes necessary for the cambium ring to increase in circumference. This is accomplished by the radial division of some of the cells of the ring to form new cambium cells. This results in the vascular rays becoming wider apart so that the tracheids, tracheal tubes and other elements of the xylem and the elements of the phloem would come to be some distance from a vascular ray were it not for the initiation of new vascular rays by the cambium. The result is that no tissue elements of xylem and phloem are far from a vascular ray.[1]

The Cork Cambium or Phellogen.—The **cork cambium** is a lateral meristem similar in some respects to the cambium ring. Its origin is in certain cells of the cortex or rather rarely, as in the apple, (*Pyrus malus*) in the epidermis itself. When it arises in the cortex it is usually the cells just below the epidermis (generally collenchyma) which become the cork cambium. Certain of these cells become meristematic and undergo repeated tangential divisions (Fig. 71), producing daughter cells on both sides. The outer daughter cells may be transformed into cork cells and thus a layer of cork is formed beneath the epidermis. The cork cells soon die and become suberized, and as a result the epidermal cells are cut off from water and food supplies and do not long remain living. The inner daughter cells which are added to the cortex are cells which remain alive for some time and are otherwise similar to the cortical cells. Together they are spoken of as the **phelloderm.** The phellogen and the interfascicular cambium are spoken of as **secondary meristems,** since they originate from cells which have previously existed in the differentiated condition for some time. The primary meristems on the other hand originate in the promeristem.

Summary of the Secondary Growth of a Woody Dicotyledon-Gymnosperm Type of Stem.—Due to the activities of the vascular cambium and the cork cambium there may be added to the stem each year the following:

[1] The term medullary ray has been so long and universally used to include both pith rays and vascular rays and the distinction between these two kinds of rays is so fundamental that it seems best to give up entirely the use of the older and more inclusive term rather than to restrict its use to pith rays.

By the vascular cambium:

1. New xylem on the outside of the old xylem.
2. New phloem on the inside of the old phloem.
3. Vascular rays in both xylem and phloem.
4. In dictyostele stems, additions to pith ray tissue on both sides of the interfascicular cambium.

By the cork cambium, or cambiums:

5. Cork on the outside of the cork cambium.
6. Phelloderm on the inside of the cork cambium.

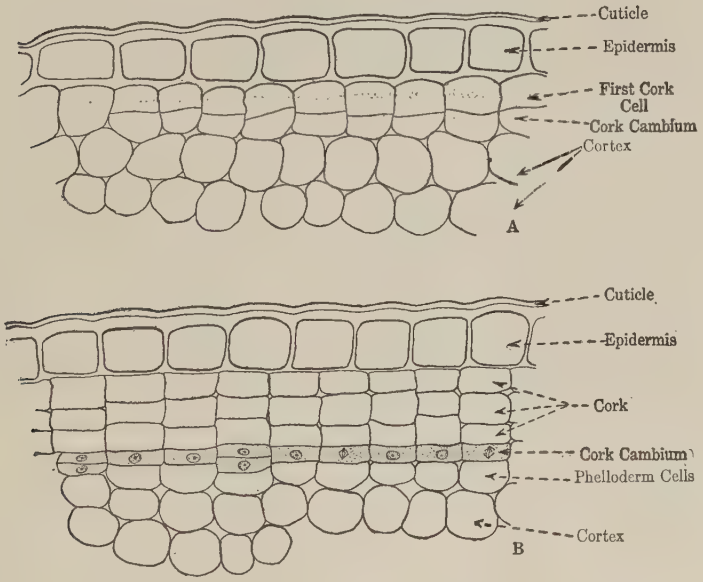


FIG. 71.—Cross sections of portions of a stem showing origin of cork cambium (*A*), and the development of cork and phelloderm from cork cambium (*B*).

Annual Rings.—In temperate climates a season of cambial activity alternates with a period of inactivity. Each growing season, there is produced by the cambium ring a band of wood. As seen on the end of a log these layers appear as concentric rings. These are the annual rings to which reference has already been made.

Any one annual ring consists of two parts which are more or less readily distinguishable. These are the inner or **spring wood** and the outer or **summer wood.** In the spring wood of dicotyledons, the tracheal tubes are usually large and quite numerous; in the summer wood, tracheal tubes are relatively smaller and fewer. The tracheids

and wood fibers of spring wood are relatively less abundant and thinner walled than those of summer wood. The summer wood of one year

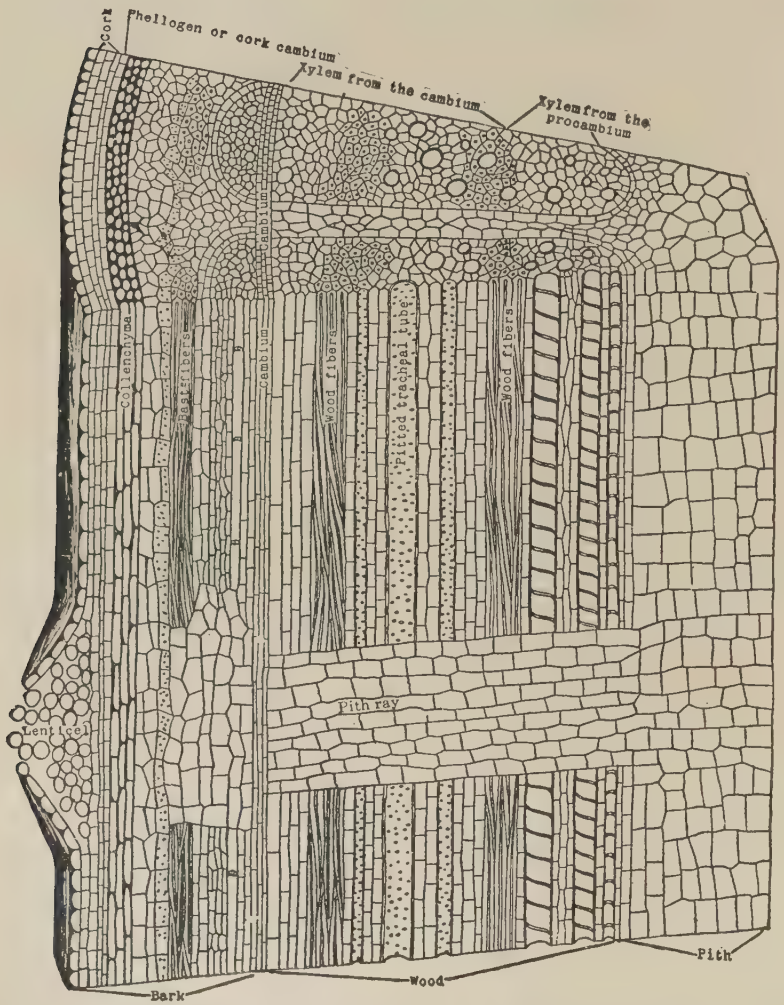


FIG. 72.—Diagram showing the topography of a dicotyledonous stem in which additions of tissues (secondary growth) have been made through the activity of vascular cambium and cork cambium. (After Stevens.)

(1923, for example) adjoins the spring wood of the following year (1924). Hence, small, thick-walled elements of the summer growth of

one year are adjacent to the relatively large, thin-walled wood elements of the spring growth of the following year, and the sharp line of demarcation between them is visible even to the naked eye (Fig. 76).

FIG. 73.—Cross section of a log of redwood (*Sequoia sempervirens*) showing annual rings, light-colored sapwood, and dark-colored heartwood. Note the radial splitting which gives evidence of greater tangential than radial shrinkage of the cells during drying. (From Division of Forestry, College of Agriculture of the University of California.)

In gymnosperms, tracheae are wholly absent and annual rings are the results of differences in the tracheids, which constitute the bulk of the wood or xylem. The tracheids laid down in summer and fall, as

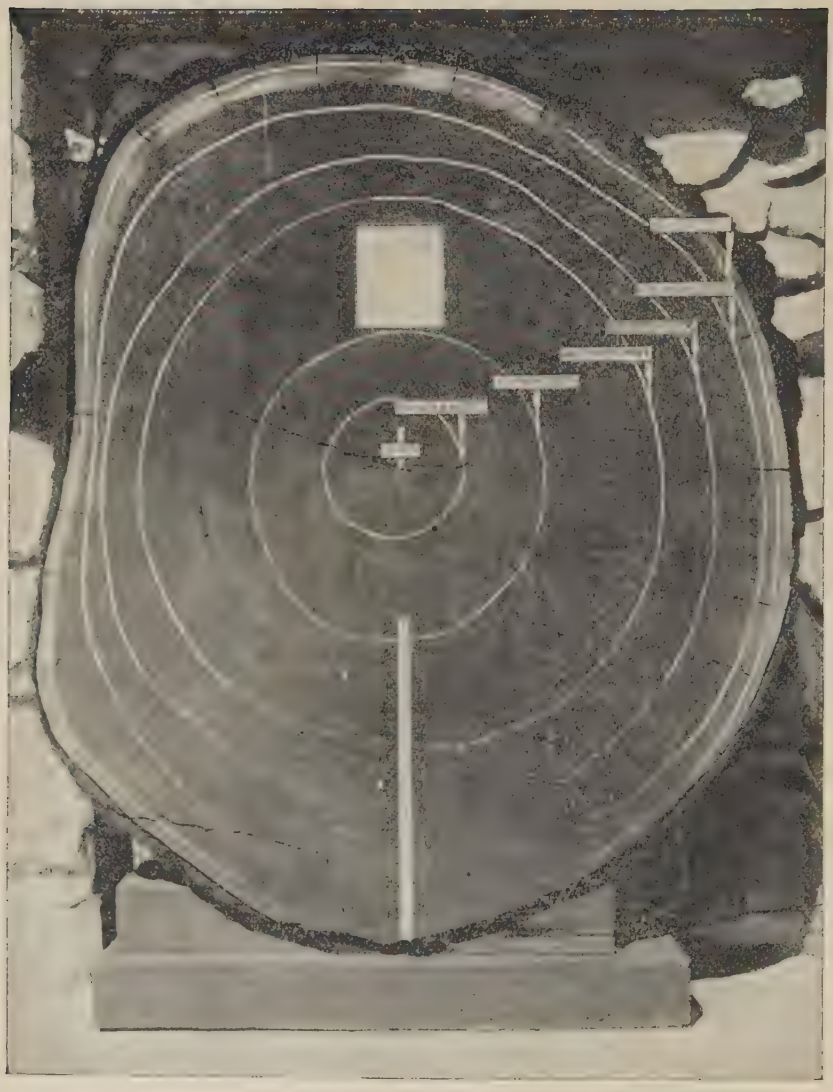


FIG. 74.—A cross section of the trunk of a relatively young tree of *Sequoia gigantea* (Big tree). The chalk lines and the arrows, except the central one, indicate approximately the annual rings formed in the years during which a number of events of great historic importance took place. The tree from which the section was cut began its growth in about A.D. 923 and was about 1000 years old when cut. There are trees now standing which are certainly twice that age and probably living trees 3000 years old exist.

compared with those formed in spring, are smaller, have thicker walls and are often radially flattened.

There is variation in the width of different growth or annual rings in the same stem. This variation is due to differences in light, heat, moisture, and other external conditions. If we could read it we would find that much of the history of a tree is recorded in its cross section.

Determining the Age of Felled Trees.—We have seen that each year a tree adds a new band of wood, called an **annual ring,** and that on account of the difference between the spring and the summer wood these rings are clearly marked. The number of annual rings seen in a cross section of a tree generally indicates the age of the trunk at that height. The number of annual rings decreases from the base of the trunk to its apex. For example, it is only in sections cut through at the base of a ten-year old tree that ten annual rings will be seen. Any section at

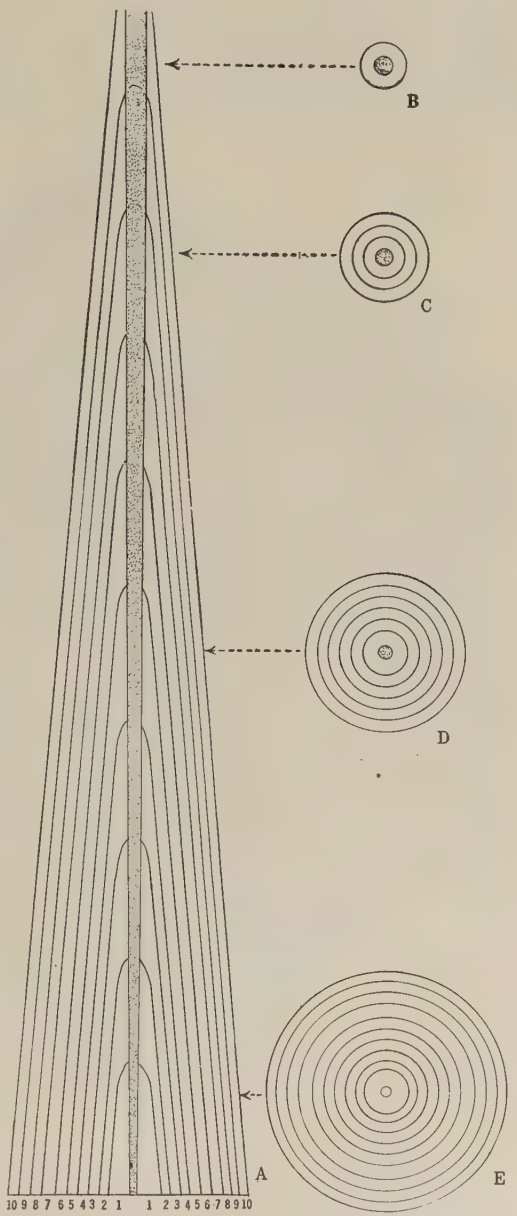


FIG. 75.—Diagram showing longitudinal and cross sections of a ten-year old tree. Note the decrease in the number of annual rings from the base of the trunk to the apex.

the base of the tree within the limits of the growth in length made by the plant during its first year, will show ten annual rings. A section through that portion of the tree which was added to its length the second year will show nine annual rings; thus, in sections through

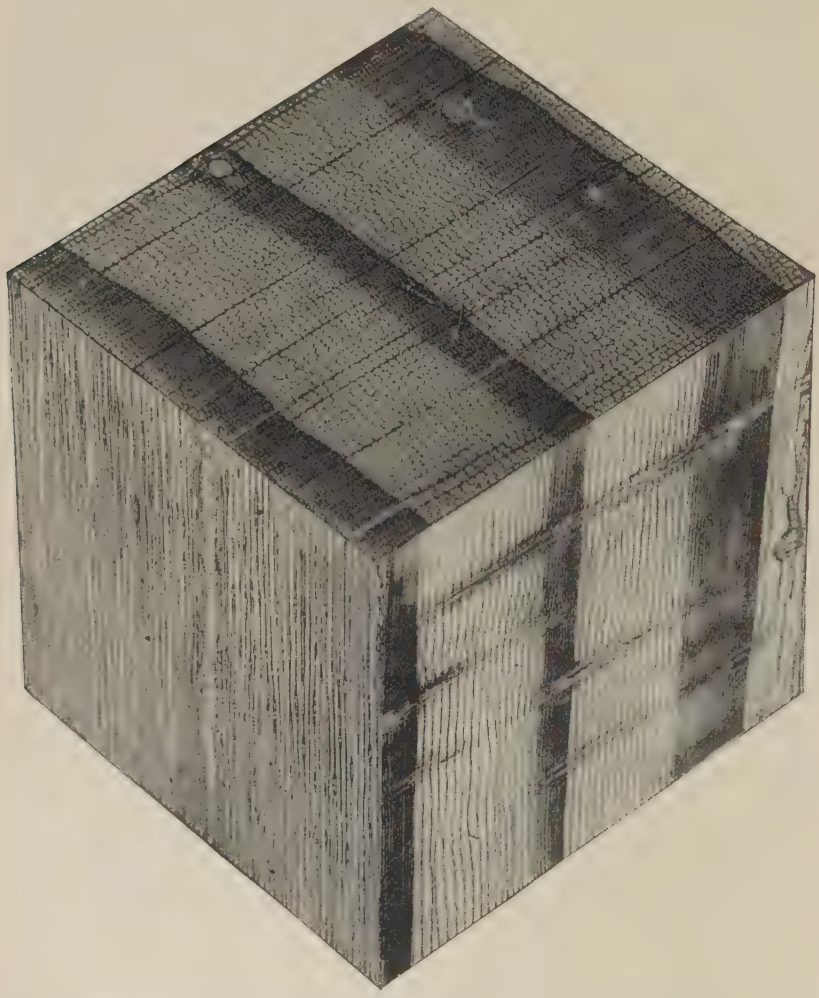


FIG. 76.—Model of block of pine wood, showing surfaces exposed by cross section (top) tangential section (left side), and radial section (right side).

the growth of the third year and each succeeding year, to the tenth, the number of annual rings will be eight, seven, six, etc., decreasing by one each year. The twig growth made the tenth year will show only one ring of wood (Fig. 75).

During the growing season, a drought or an insect attack may interrupt the activity of the cambium by destroying the foliage. Later, the tree may produce a new crop of leaves and these will enable the cambium to become active again and to develop a new ring of wood. Thus,

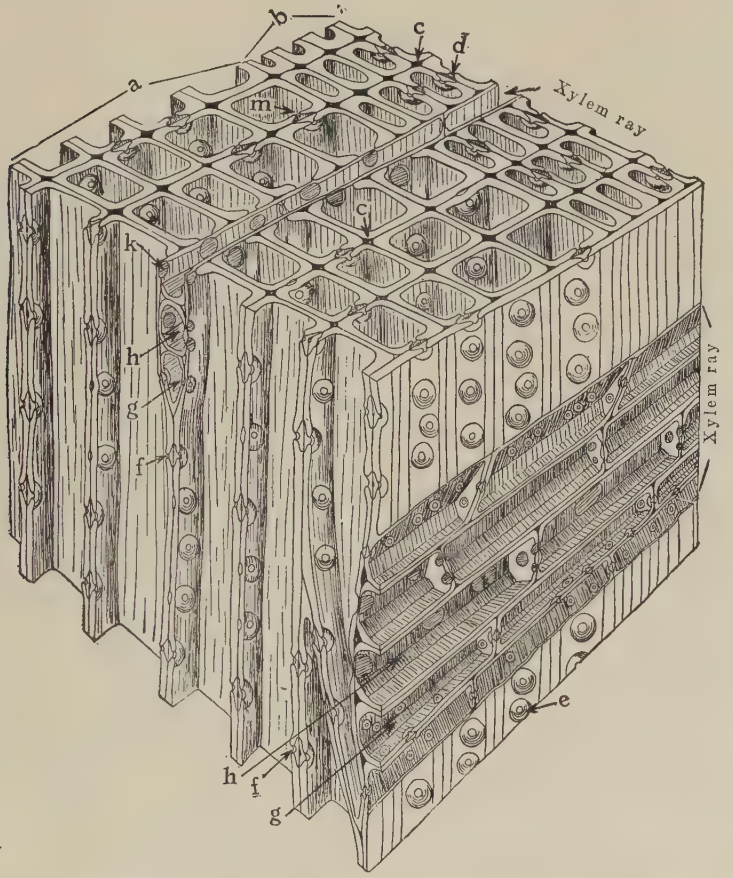


FIG. 77.—Diagram showing block of pine wood. *a*, spring wood; *b*, summer wood; *c*, intercellular space; *d*, bordered pit in tangential wall of summer wood; *m*, *f*, and *e*, bordered pits in radial wall of spring wood; *h* and *g*, pith ray cells *k*, thin place in radial wall of pith ray cell. (After Stevens.)

in a single season two rings of wood may be formed. These extra rings may lead to inaccuracies in estimating the age of a tree by counting the rings. Such extra rings, however, are not often produced.

Wood.—We have used the term wood for the xylem part of the stele. From the forester's or lumberman's standpoint, wood is any part of the

stem exclusive of the bark (tissue outside of cambium). Let us study the structure of the wood of an old stem (trunk) by an examination of cross, radial and tangential sections.

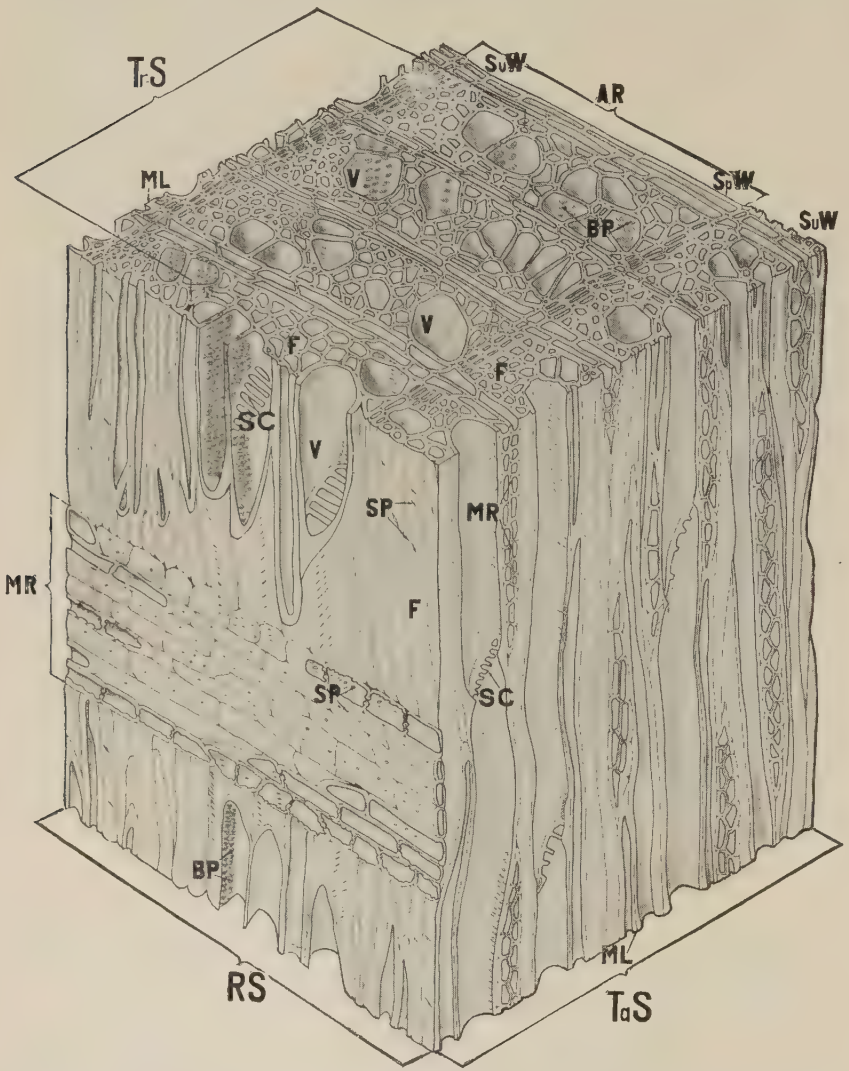


FIG. 78.—Diagram of a typical hardwood. *TrS*, cross section; *RS*, radial section; *TaS*, tangential section; *AR*, annual ring; *SuW*, summer wood; *SpW*, springwood; *MR*, xylem ray; *V*, vessel; *F*, wood fiber; *SP*, simple pits; *BP*, bordered pits; *SC*, sclariform perforations; *ML*, middle lamella. (After chart by U. S. Forest Products Laboratory.)

Cross Section.—In cross section, the annual rings appear as more or less parallel bands, each with spring and summer wood. The wood rays are seen as narrow radial lines crossing the annual rings at right angles. The tracheal tubes, tracheids, wood fibers, and wood parenchyma have their long axes running longitudinally and accordingly in cross section the cavities of the tracheal tubes appear as large rounded pores; the tracheids and wood fibers are seen as much smaller and thicker-walled elements which are polygonal or square in shape; the wood parenchyma cells resemble wood fibers and tracheids in cross section but have thinner walls.

Radial Section.—The annual rings appear in radial section as more or less parallel bands which impart to the wood its characteristic grain. **Coarse-grain** wood is wood with wide annual rings while **fine-grain** wood has narrow rings. Wood rays, as seen in radial section, appear as bands or bars of varying width and length, running at right angles to the tracheal tubes, tracheids, and wood fibers. Tracheal tubes appear as long narrow grooves.

A quarter-sawed board is simply a thick radial section. The beauty of quartered oak and other woods is due to the luster of large wood rays, when cut radially.

Tangential Section.—In tangential section, the annual rings appear as wide bands, which may form various irregular figures. The wood rays are cut across and appear as lens-shaped groups of cells. Tracheal tubes, wood fibers, tracheids, and wood parenchyma appear much as they do in radial section.

Heartwood and Sapwood.—If we examine the cut end of a log, we observe that the woody cylinder consists of a light-colored outer zone, the **sapwood,** surrounding a darker colored zone, the **heartwood.** Sapwood is composed of elements some of which, chiefly the wood parenchyma cells, are still alive, whereas heartwood consists of elements, all of which are dead. The darker color of heartwood of most trees is largely due to the deposition in the cell walls and cell cavities of resins, gums, tannin, certain pigments, and other substances. These depositions increase the weight, hardness, and durability of the heartwood, and they also plug up the conducting elements and thus retard or entirely stop the movement of sap. Transport of sap is almost entirely confined to the sapwood. The loss of the conducting power of the tracheal tubes and tracheids of the heartwood is due to the plugging of these elements, not only by the substances mentioned above, but also by **tyloses.** These are formed while the parenchyma cells are still alive. Where such cells are in contact with tracheids or tracheal tubes, their protoplasts may break through the thin portions of the walls of the con-

ducting elements and thus form protrusions (tyloses) in the cavities of the latter (Fig. 85).

Bark.—All the tissue outside of the vascular cambium is included under the term bark. The bark is readily separated from the woody

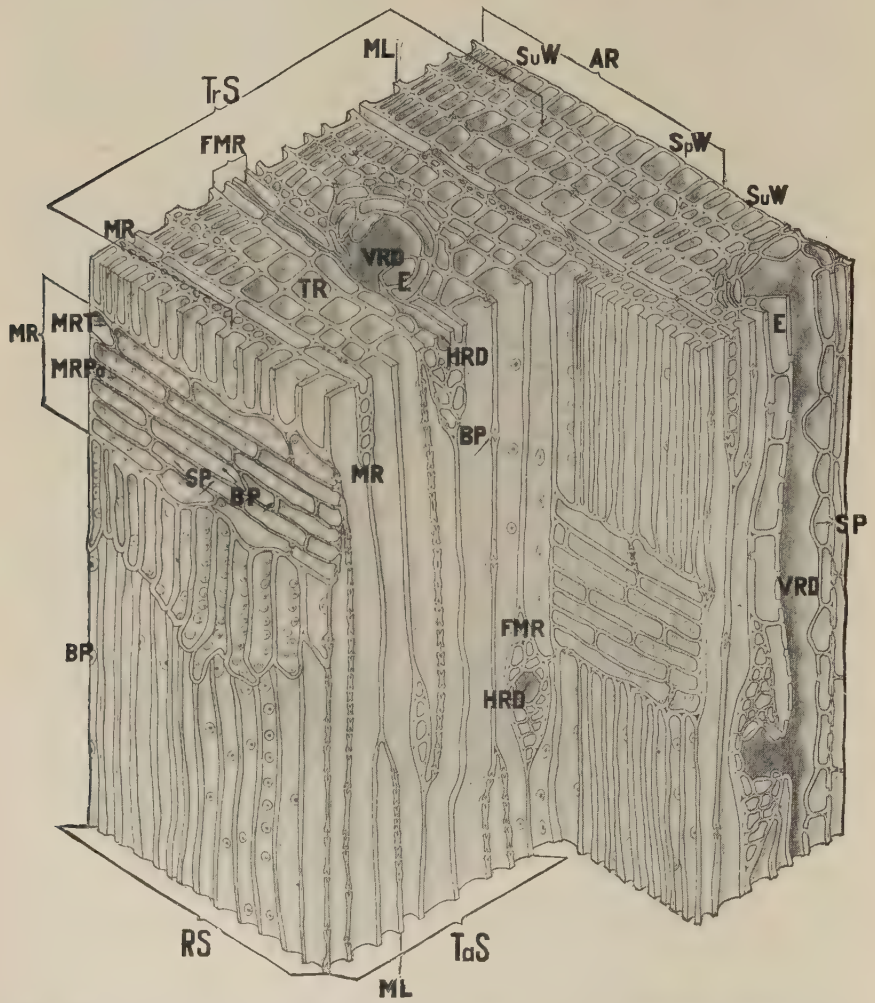


FIG. 79.—Diagram of a typical coniferous wood. *TrS*, transverse section; *RS*, radial section; *TaS*, tangential section; *AR*, annual ring; *SuW*, summer wood; *SpW*, spring wood; *MR*, xylem ray; *TR*, wood tracheids; *E*, secretory cell; *TMR*, fusiform xylem ray; *MRPa*, xylem ray parenchyma; *SP*, simple pits; *BP*, bordered pits; *HRD*, horizontal resin duct; *VRT*, vertical resin duct; *MRT*, xylem ray tracheids; *ML*, primary wall. (After chart by United States Forest Products Laboratory.)

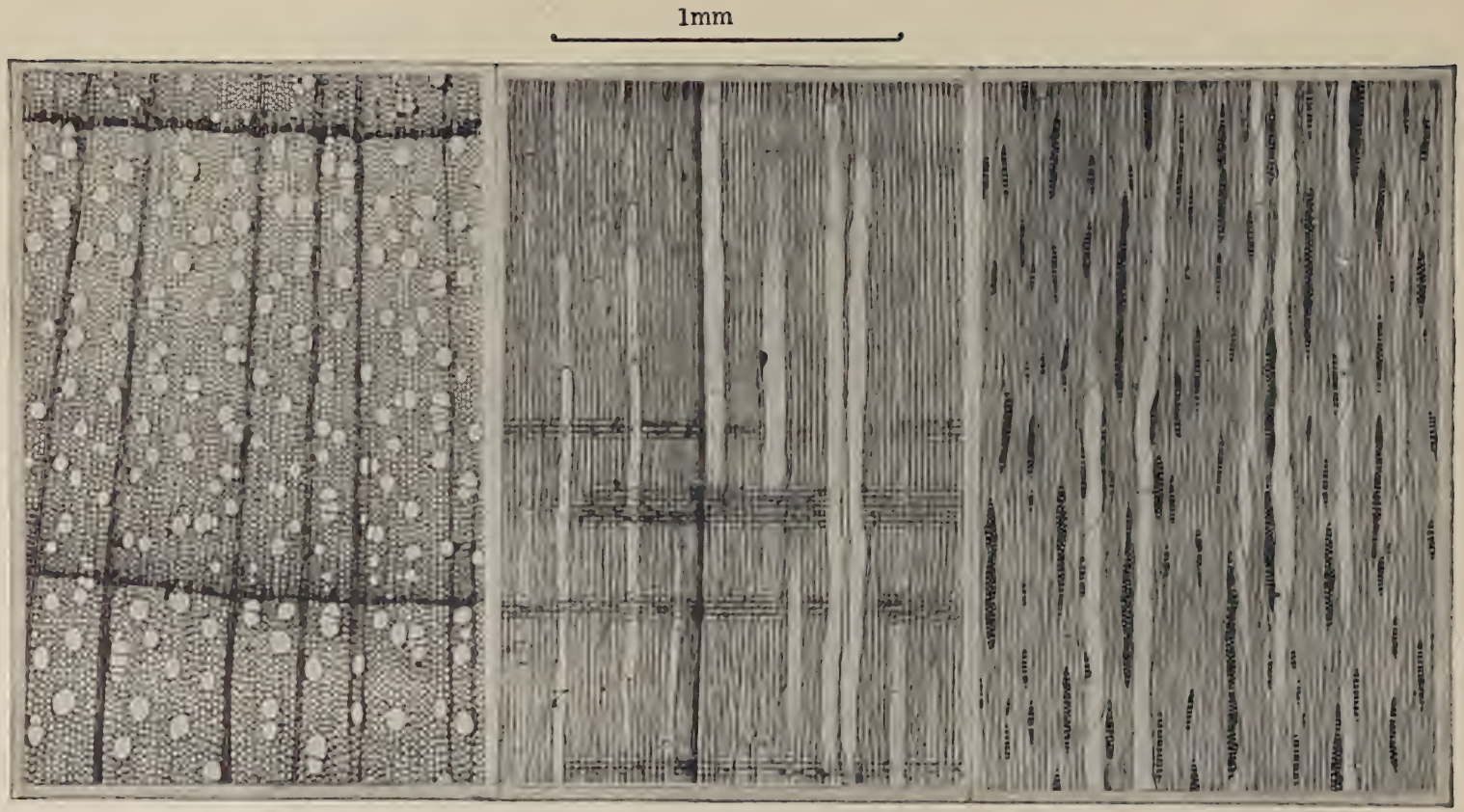


FIG. 80.—Cross (left), radial (middle), and tangential (right) sections of the wood of hard maple (*Acer saccharum*). (Photographs by United States Forest Products Laboratory, Madison, Wis.)

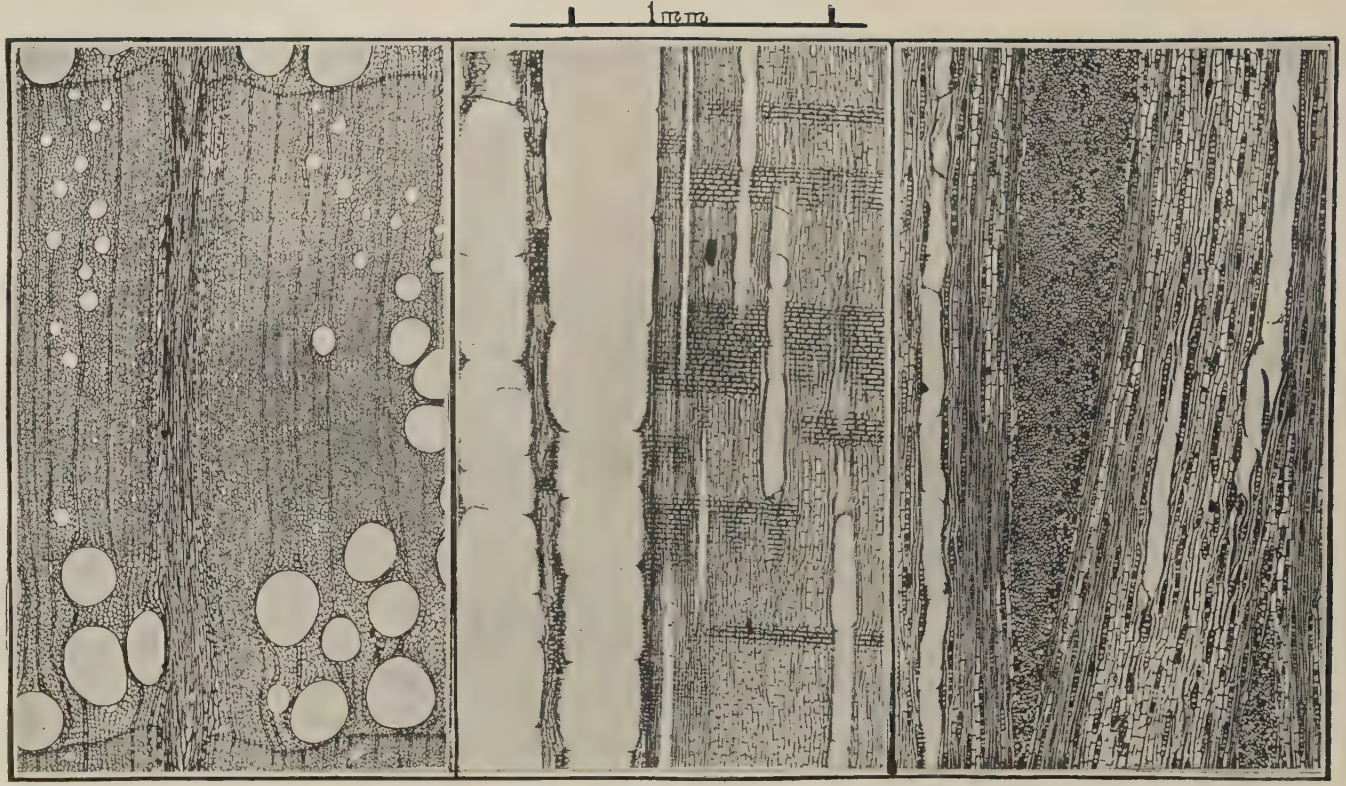


FIG. 81.—Cross (left), radial (middle), and tangential (right), sections of the wood of red oak (*Quercus rubra*). (Photographs by United Forest Products Laboratory, Madison, Wis.)

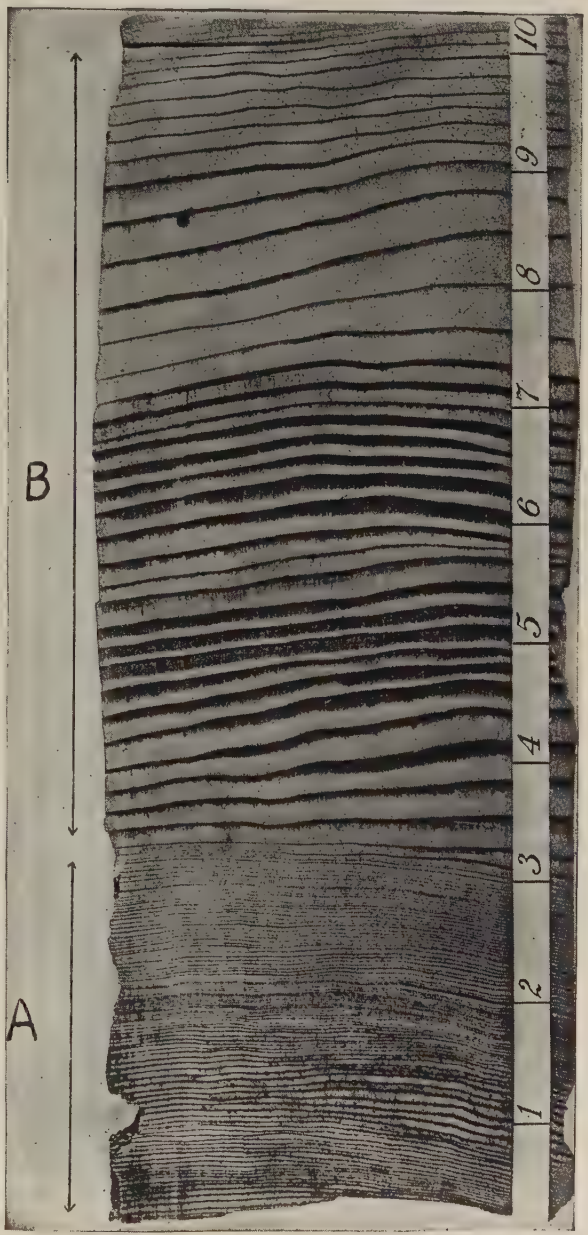


FIG. 82.—Cross section of a part of a redwood log showing the effect of external conditions on the width of growth rings. The portion of the wood marked "A" was produced during a period of about eighty years. That marked "B" was produced during a period of about forty years. Up to the time of the increase in ring width the tree grew under unfavorable conditions crowded and shaded by larger trees which surrounded it. The surrounding trees were then felled by lumbermen and in the following forty years the increase in stem diameter was almost four times that during the preceding eighty years. (Photograph by the Forestry Division, College of Agriculture, of the University of California.)

cylinder, due to the fact that the walls of the cambium cells are thin and easily ruptured. The bark is made up of the following tissues: cork, cork cambium, phelloderm, cortex, pericycle and phloem. As a stem grows older, this original cork cambium may cease its activity and a

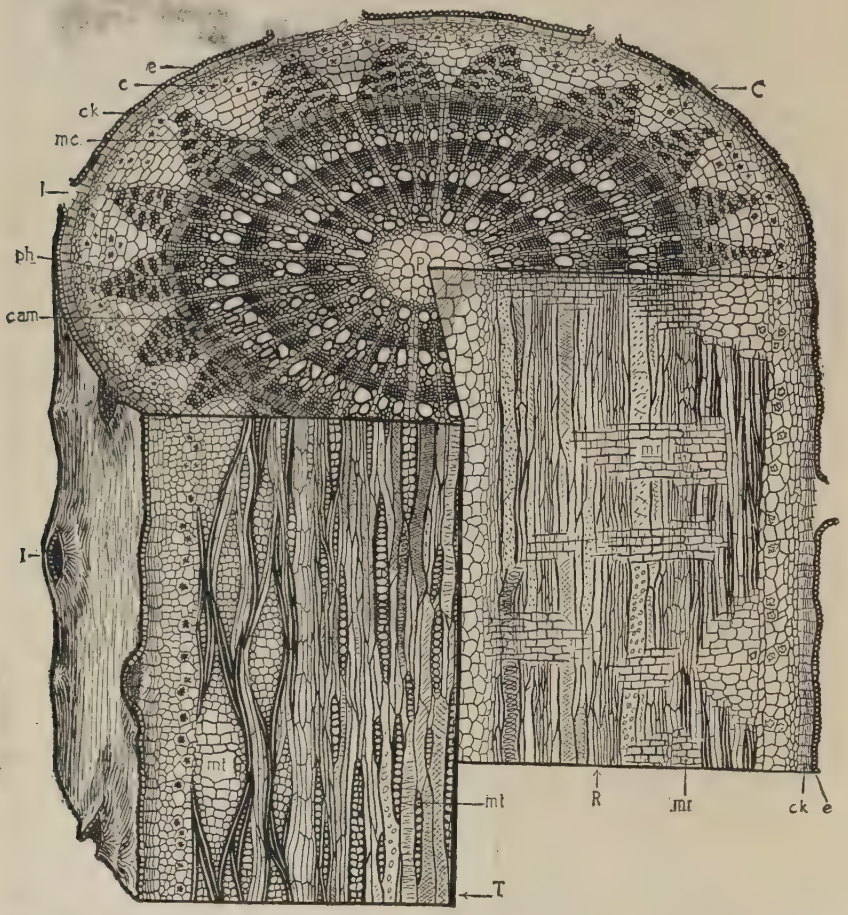


FIG. 83.—Diagram of a three-year-old stem of basswood (*Tilia*). Cross (*C*), radial (*R*) and tangential (*T*) views are shown. *C*, cortex; *ck*, cork; *ph*, phloem with darker bands of bast fibers; *mc*, cross-section of pith ray; *mr*, radial section of pith ray; *mt*, tangential section of pith ray; *l*, lenticels; *cam*, cambium cylinder; *P*, pith. (After Curtis.)

new cork cambium may be formed deeper in the cortex. Subsequently, new cork cambiums may appear at successively lower levels. In a very old stem, the cork cambium may be formed even as deep in the bark as the phloem. In plants in which the original cork cambium

FIG. 84.—Wawona tunnel tree (*Sequoia gigantea*) in Mariposa Grove, Yosemite National Park. The tree is still living although most of the heartwood at the base of the tree has been cut away. Transport of sap is largely confined to the sapwood.

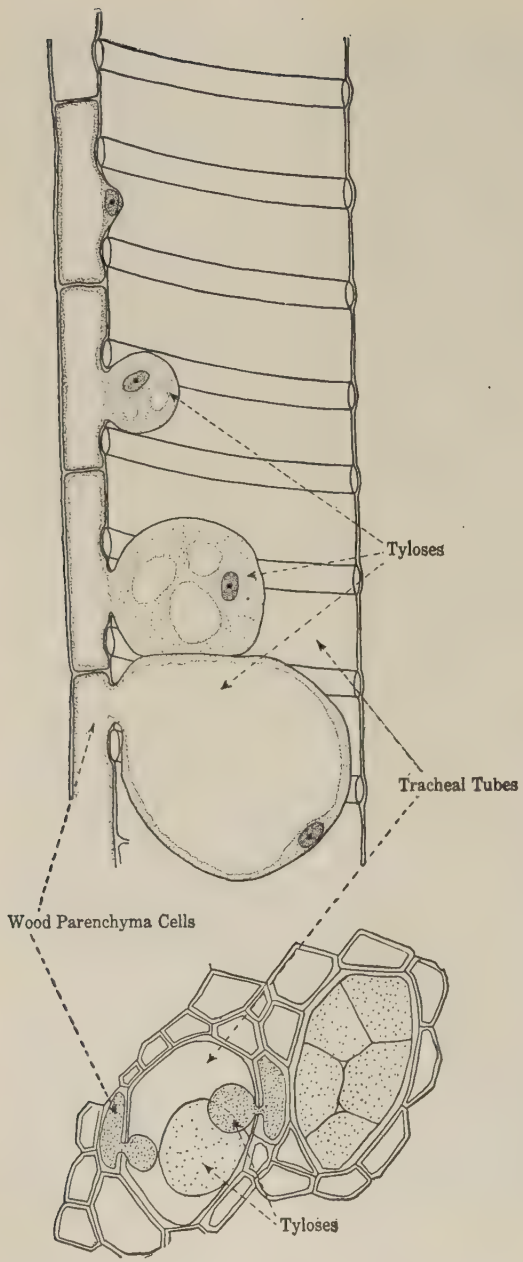


FIG. 85.—Tyloses in various stages of development in the tracheal tubes of black locust (*Robinia pseudacacia*).

remains active for years there may frequently be seen (as in the cork of *Aristolochia*) conspicuous layers or "annual rings" corresponding to variations in the seasonal activity of the cork cambium. It will be recalled that cork is made up of dead cells with suberized walls and that this tissue is therefore highly impermeable to water and dissolved substances. Consequently, any living cells outside the corky layer will soon die.

As a result of the increase in stem circumference through the activities of the cambium layers, the outer cork layers are stretched and may finally split. These layers may soon become detached from the stem, leaving the surface of the bark smooth, as in the sycamore (*Platanus*). In other plants, such as the oak (*Quercus*) and the elm (*Ulmus*), they may remain attached for a number of years, thus forming a thick bark which is generally broken into characteristic furrows.

The cork replaces the epidermis as a protective tissue. It shields

tissues beneath from mechanical injury, prevents the entrance of insect and fungous parasites, and on account of its poor conduction of heat, protects the underlying tissues from sudden changes of temperature. Most important of all, as a waterproof covering, cork has no equal. It is this property which is made use of when we utilize cork to close bottles containing liquids. The value of cork in checking water loss is also well shown in the case of the potato tuber, which is covered by a thin layer of cork. It has been determined that a peeled potato tuber may lose in twenty-four hours over sixty times as much water as it did in the same period before it was peeled.

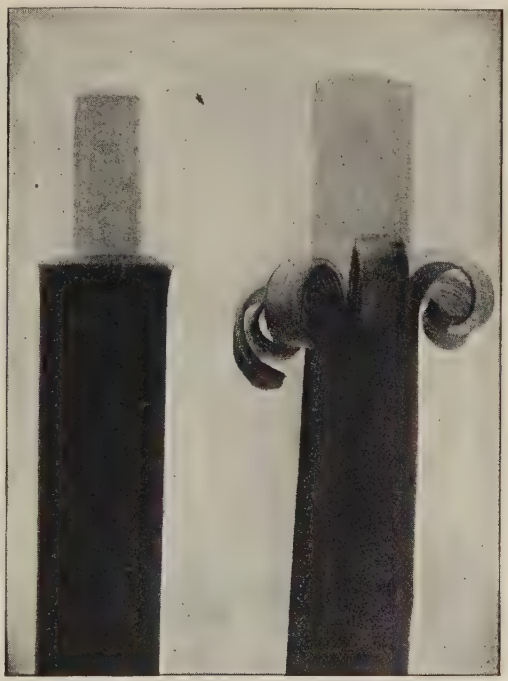


FIG. 86.—Flower stalks of Calla lily (*Richardia*) in which a central cylinder of tissue has been freed from the tissue around it but left intact at the base, in order to demonstrate the tissue tensions which exist in many plant organs. In the case of each of the two flower stalks, after trimming the end off square with a razor the cylinder of tissue was freed from the outer tissue to a depth 10 centimeters by means of a sharp, thoroughly wetted cork borer. In the case of the stalk to the right the outer tissue was then cut into lengthwise strips which were left attached at the base.

Lenticels.—In very young parts of stems, gases may enter and leave through the stomata of the epidermis. When cork is formed beneath the epidermis this impervious layer tends to cut off communication between the stomata and the cells of the cortex. This would prevent the access of oxygen to the cells which underlie the cork, were it not for special ventilating regions in the cork. It is always just beneath a stoma that such regions are formed. There, the cork cambium cells may give rise, not to typical cork cells, but instead to large thin-walled cells among which are intercellular spaces. These masses of tissue, which by enlargement finally break through the epidermis and project slightly above the surface of the stem, are known as lenticels (Fig. 87).

They permit a ready exchange of gases between the atmosphere and the intercellular spaces of the tissues beneath the cork. Lenticels are especially conspicuous in such plants as plum and cherry (*Prunus*), and in birch (*Betula*).

The Herbaceous Dicotyledon Type of Stem.—Herbaceous dicotyledonous stems are similar to woody dicotyledonous-gymnosperm stems in the development of their tissues from the promeristem and the primary meristems. In structure they resemble closely young portions of the woody stems of the dicotyledon-gymnosperm type. The amount of vascular tissue is generally relatively less and the pith and the cortex relatively greater in extent than in woody stems. As in the woody dicotyledon-gymnosperm stem both siphonosteles and dictyo-

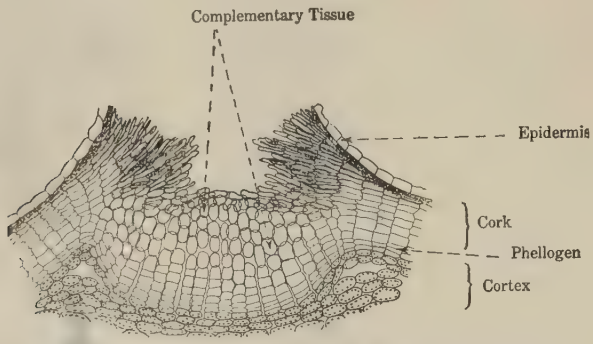


FIG. 87.—Transverse section of lenticel of two-year old stem of elder. (*Sambucus nigra*. (After Haberlandt.)

steles are found. The latter type with its distinct vascular bundles separated by pith rays and with or without interfascicular cambium, occurs somewhat more frequently among species with herbaceous stems than it does in woody stemmed plants. In some cases the vascular tissue is in distinct bundles near the top of the stem and in a hollow cylinder near the base.

The Monocotyledon Type of Stem.—As in the stem types already discussed the promeristem of the growing point of monocotyledons, corn for example, differentiates into protoderm, procambium and ground peristem. The protoderm becomes a single epidermal layer which does not differ essentially from that of other seed plants. The procambium always occurs in numerous strands scattered throughout the ground meristem, and remains thus, never forming a ring or hollow cylinder as it does in most gymnosperm and dicotyledon stems. All the procambium cells differentiate into xylem and phloem elements

and none remain in the meristematic condition as do those of the vascular cambium of gymnosperms and dicotyledons. Bundles of this sort, which are without a cambium, are called **closed bundles** (Fig. 92).

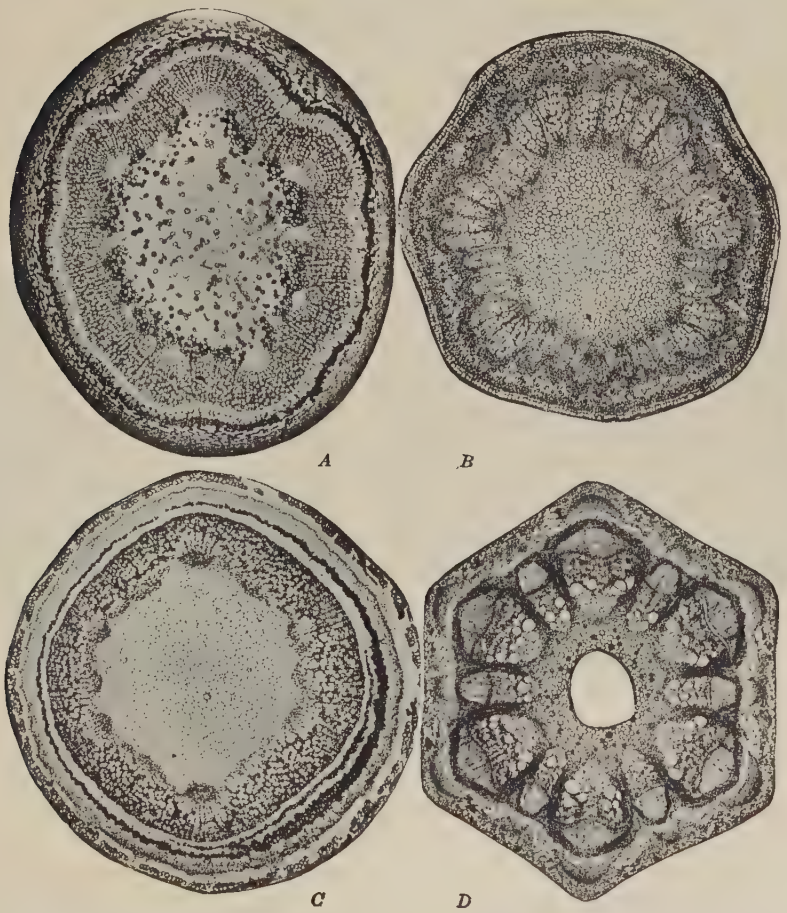


FIG. 88.—Types of dicotyledonous stems. *A*, *Liquidambar*, tree, stele continuous; *B*, *Platanus*, tree, stele dissected. *C*, *Lonicera*, woody vine, stele continuous; *D*. *Clematis*, woody vine, stele dissected. (After Sinnott and Bailey, from Eames and MacDaniels, *An Introduction to Plant Anatomy*, McGraw-Hill Book Co.)

Those of other seed-bearing plants in which a cambium lies between the xylem and the phloem are called **open bundles.**

Between the epidermis and the outermost vascular bundles is a narrow zone corresponding to the cortex and pericycle but these two regions are not distinctly marked off from each other in most monocotyledonous stems. Since there is not a ring of vascular tissue or a single circle of bundles but in most cases a large number of vascular bundles scattered through the stele, a definite pith is lacking. The stele is a dictyostele (stele with distinct vascular bundles) in contrast with the siphonosteles (with hollow vascular cylinder) of most dicotyledonous stems and with the protostele characteristic of the roots.

FIG. 89.—Types of herbaceous dicotyledonous stems (continued). *E*, *Digitalis*, herb, stele continuous. *F*, *Artemisia*, herb, stele dissected. (After Sinnott and Bailey, from Eames and MacDaniels, *An Introduction to Plant Anatomy*, McGraw-Hill Book Co.)

Due to the absence of a cambium most monocotyledonous stems are not able to add to the quantity of xylem and phloem nor to increase to any considerable extent the number of cells in any of the other tissues. Most monocotyledonous stems do not increase much in thickness as they increase in age. What growth in thickness they do have is due almost entirely to enlargement of cells differentiated from the primary meristems. In a few tree-like monocotyledons, such as Cordyline, Yucca and Aloe, a cambium ring arises in the pericycle. This cambium gives rise to new closed bundles on the inner side and also adds to the other tissues of the stem. The characteristic features of monocotyledonous stems are as follows:

(*a*) The large number of vascular bundles and their scattered distribution.

(*b*) The absence of cambium in the vascular bundles.

(*c*) The slight increase in the stem circumference on account of the absence of a cambium. The increase that does occur is mostly the result of growth in the size of cells already present. Exceptions to this general statement have already been cited.

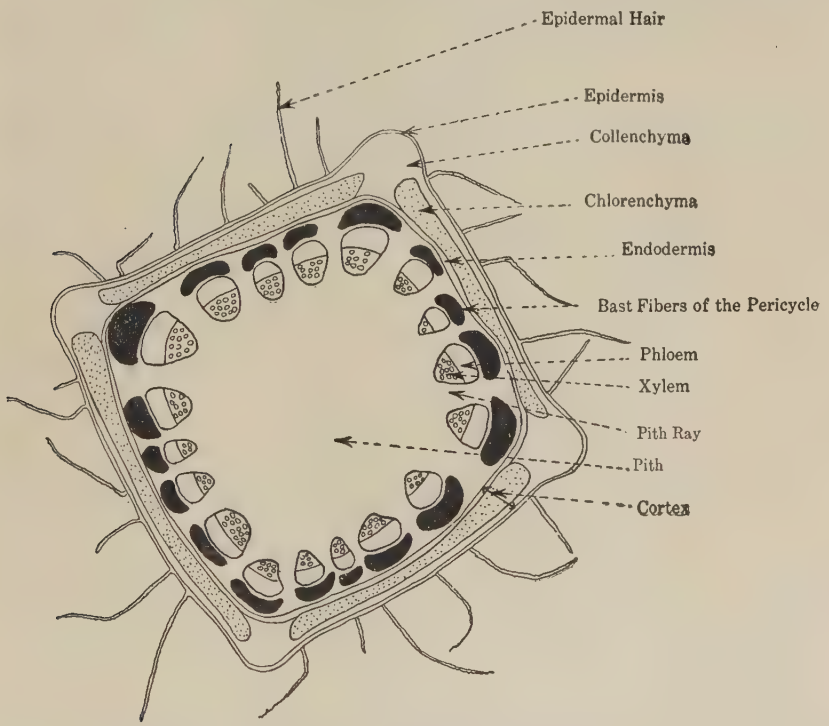


FIG. 90.—Diagram of a cross section of the stem of alfalfa (*Medicago sativa*)—an herbaceous dicotyledonous plant.

(*d*) The restricted development of the leafy crown of perennial monocotyledons, like the palms, by reason of the limited water-conducting power of the stem of monocotyledons. The latter is probably due to the fact that it is impossible for the plant to increase the number of vascular bundles or add either phloem or xylem to bundles already existing.

(*e*) The long period over which the phloem and xylem elements continue to carry on their work. Whereas in the stems of

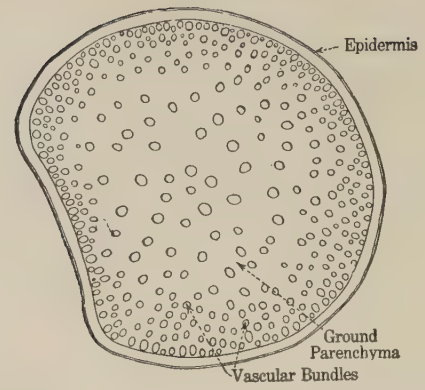


FIG. 91.—Diagrammatic cross section of the stem of corn (*Zea mays*)—an herbaceous monocotyledonous plant.

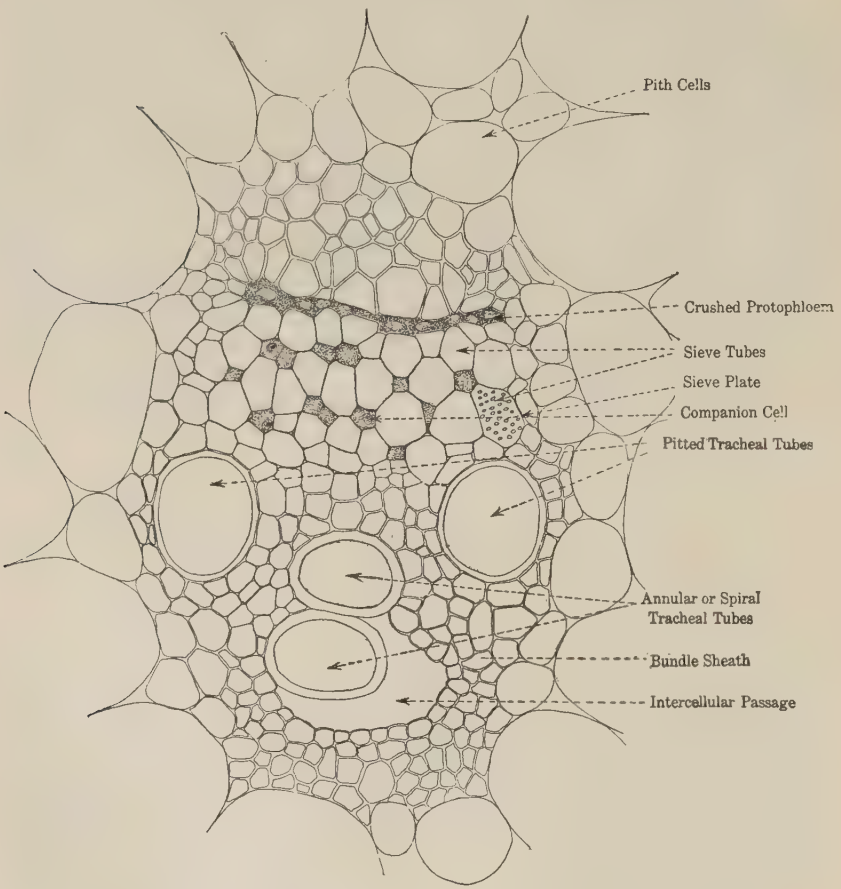


FIG. 92.—Cross section of a vascular bundle of the stem of corn (*Zea mays*)—a monocotyledon.

perennial dicotyledons and gymnosperms conductive elements may cease to function within a few years, and are replaced by younger conducting elements, in perennial monocotyledons these elements retain their ability to transport materials throughout the life of the plant.

The stems of grasses are called **culms** (Fig. 93). They are usually cylindrical in shape, and when mature their internodes are generally hollow, although they are sometimes solid, as in corn. These hollow internodes form a series of chambers which are separated

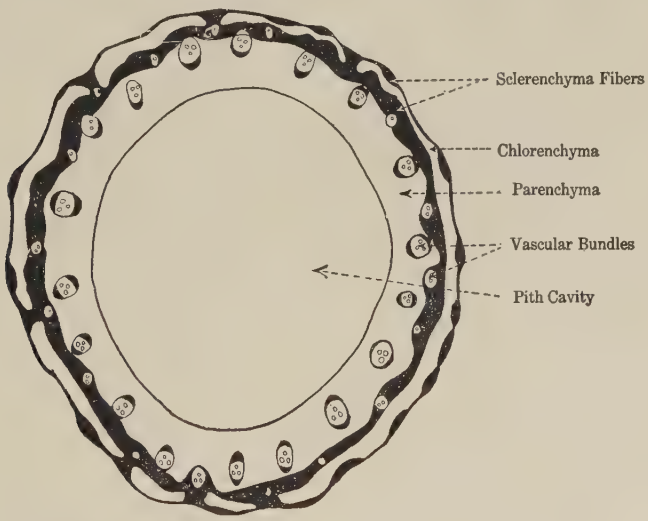


FIG. 93.—Cross section of the stem of rye (*Secale cereale*). Redrawn from Nathanson.

by partitions at the nodes. A very characteristic feature of grass stems is that the differentiation of permanent tissues from the promeristem may take place much earlier in the upper part of each internode than it does at the very base of the node. As a result the tissue just above some of the nodes often remain soft and meristematic long after the rest of the internode has its tissues fully differentiated. These meristematic regions, which are generally enclosed by the sheathing base of the leaf may later become active and add considerably to the length of the stem. It is thus that the flower cluster (young wheat head or cluster of young oats) which is finally borne at the end of the main stem of many grasses is raised above the rest of the plant.

Elongation which is thus distributed over a considerable length of an organ instead of being restricted to a part near the tip is not very

common in seed-bearing plants (Spermatophyta). It is called **intercalary growth** in contrast with the much more usual **apical growth.** Meristematic regions, left behind so to speak, here and there along the stem and able to later bring about growth in length are called **intercalary meristems** in contrast with apical meristems and with the lateral meristems (vascular cambium and cork cambium), which increase the thickness of stems.

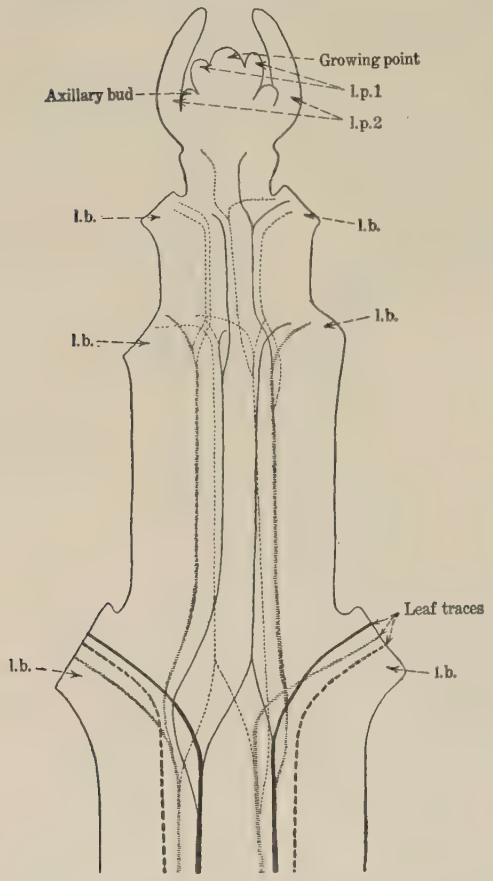


FIG. 94.—*Clematis* species. Diagram of dictyostele stem of a dicotyledon, *Clematis*, showing the growing point and, in perspective, the vascular bundles of the stem and the vascular bundles (leaf traces) which pass out into the leaves at the nodes. (After Nägeli).

The Anatomy of Stems at Nodes.—Throughout our account of the structure of stems we have discussed the arrangement of tissues in the internodes but have had nothing to say of the anatomy of the nodes. It is at the nodes that groups of xylem and phloem elements (vascular bundles) enter the stem from the leaves and join the vascular tissue of the stele. Sometimes the leaf vascular bundles (**leaf traces**) pass downward through one or several internodes before joining the vascular cylinder or bundles of the stem. Naturally the arrangement of tissues is much more complex and difficult to make out in sections of nodes than of internodes. The number of **leaf traces,** in the leaf stalk (petiole), varies in number from one to five or more. In the leaf blade these branch repeatedly and form the veins. Thus there is vascular connection between all the permanent tissues of the plant from the margins of the leaves almost to the tips of the smallest roots and to the growing points of all the buds and branches of the stem.

FUNCTIONS OF STEMS

The primary functions of the stem are **support** of the leaves and **conduction** of water and raw materials for food manufacture to the leaves, and of food from the leaves. Secondary functions, that is those functions which the stem may carry on but which are at least equally characteristic of other organs, are **food storage** and **food manufacture.**

Support.—The stem supports the leaves and so distributes them through space that they are in positions favorable for light absorption and thus conducive to photosynthesis. The elevation of the flowers on the stem favors the transfer of pollen both by wind and insects as well as the dissemination of seeds.

Conduction.—The stem conducts (*a*) water absorbed by the root from the soil, (*b*) dissolved inorganic substances also taken up from the soil by roots, and (*c*) various foods manufactured in the plant. In monocotyledons and dicotyledons the tracheal tubes are the chief carriers of water and inorganic salts from the roots to the leaves. This function is shared, however, by the tracheids, and in the gymnosperms which lack tracheal tubes, tracheids are the only elements which conduct water and inorganic salts longitudinally.

The rate of movement of water up the stem may be roughly ascertained by placing a leafy branch, which has been cut under water, in a solution of eosin, indigo carmine, or any one of various other dyes. If after a short period the stem is split lengthwise, or if cross sections are cut, the height to which the solution has risen can be determined. By similar methods, the great botanist Sachs found, for example, that in the tobacco plant water conduction might go on at as rapid a rate as 118 centimeters an hour.

The Path of Movement of Sap.—By the method just described, the path of movement of water and the inorganic salts dissolved in it up the stem may also be determined. After a branch has been in the colored solution a short time, cross and longitudinal sections will show that the solution is present only in the tracheal tubes and tracheids. That the tissues outside the woody cylinder, including the sieve tubes, are not essential to the rise of sap may also be shown by the fact that complete girdling is not followed by wilting of leaves above the girdled portion. By complete girdling is meant the removal of cork or epidermis, cortex, pericycle, phloem and cambium. The pith may also be destroyed without interrupting water conduction. Well fitted as the tracheids and tracheal tubes are by their elongation in the vertical direction for the conduction of water and inorganic salts longitudinally in the stem they are not able to conduct efficiently across the stem. Yet

transfer of water from the wood to the phloem, pericycle, cortex, phelloderm and phellogen is essential. It is probably the wood parenchyma cells and the vascular rays (also pith rays when present) through which this radial movement of water principally goes on. Where a tracheid or tracheal tube comes into contact with a vascular ray or wood parenchyma cell, pits are usually found in the common wall between them, which make easy the passage of sap.

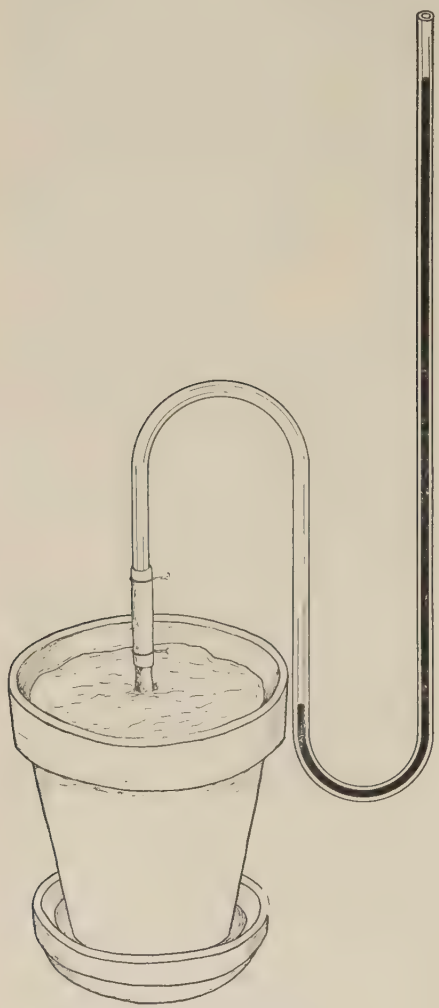


FIG. 95.—Apparatus for demonstrating root pressure. The difference in the elevation of the mercury in the arms of the U-tube is a measure of the root pressure in the decapitated plant.

The Factors Responsible for the Rise of Sap in Stems.—The quantity of water which may be transpired from a tree in a single growing season and which must therefore be conducted up the stem during that time is astonishingly great. Thus it has been shown that a hundred year old beech tree, bearing perhaps a quarter of a million leaves, may lose in the six months from June to November inclusive, as much as 9000 kilograms of water or on the average over 45 kilograms (or liters) daily. In view of the fact that such large quantities of water pass upward daily through the trunks of large trees and that this water is often raised to great heights (100 meters or more in some Australian species of Eucalyptus and up to 115 meters in *Sequoia sempervirens*) it seems only natural that the rise of sap should have been the subject of much speculation and study. The question as to what causes the sap to rise is however still unsettled. We shall

briefly discuss a few of the many explanations which have been advanced.

Root Pressure.—The absorption of water by the roots sets up a pressure in the conducting tissue which is known as **root pressure.** This may be easily demonstrated by cutting off the main stem of a vigorously growing plant several inches above the ground and replacing it by a glass tube attached by rubber tubing (Fig. 95). After a time, if the plant is kept well watered, sufficient pressure may develop to raise the sap in the tube to a height of several meters. This root pressure may be sufficient in some plants to raise water as high as 15 meters. Such high pressures, which are of rare occurrence, are however quite insufficient to explain the rise of sap to the tops of tall trees. A second and apparently quite valid objection to the root pressure theory is that even trees in which such high root pressures may under favorable conditions exist show no root pressure at all when they are transpiring freely and therefore conducting water most actively. If the stems of actively transpiring plants are cut across, no water escapes from the cut surfaces as should be the case if the water is being forced up the stem by root pressure. On the contrary air is at once drawn into the tracheids and tracheal tubes when the stem is severed which shows clearly that the sap was being pulled up from above, not pushed up from below.

Capillarity.—It is a familiar fact that in fine tubes liquids capable of wetting the material of which the tubes are made will rise. The height to which the liquid will rise is greater the smaller the bore of the tubes. It is due to this property of capillarity that oil rises in the irregular tubes between the fibers of a wick. It has been suggested that water may rise by capillarity in the tracheal tubes and tracheids of the stem. There

FIG. 96.—Method of demonstrating the lifting power of a transpiring leaf surface. The elevation of the mercury column in the glass tube above that in the dish is a measure of this power.

are many objections to this theory of which two only need be mentioned. First, tracheal tubes and tracheids are not nearly fine enough in bore to raise water by capillarity to the top of even a very small tree, and second, the viscosity of water is such that in tubes of such fineness as would be theoretically necessary to raise water to the top of a tree of moderate height, water would not move at all unless immense pressures were exerted upon it.

Action of Living Cells of the Wood.—It was long ago suggested that the living cells adjoining the tracheal tubes and tracheids are able to draw sap from conducting elements below and force it upward into tracheids and tracheal tubes above. Various experiments in which the tissues of a portion of the stem were killed either by heat or poisonous substances and in which leaves above the killed region remained fresh for some time seem to disprove this theory of the pumping action of the living cells of the wood. It still has its ardent defenders nevertheless.

Transpiration Pull and Water Cohesion.—This theory of sap rise seems to be the most satisfactory thus far advanced. It rests first, upon the fact that loss of water by transpiration from the cells of the leaf tends to maintain a high concentration of solutes in these cells which results in the leaf cells withdrawing water from the dilute solution (sap) in the tracheids. Accordingly, a pull is exerted on the upper end of the water column in the conducting elements and the entire sap stream is raised. This explanation requires that there be a continuous water column from root to leaf and that this water column have sufficient tensile strength to hold itself intact, that is to say, to prevent its breaking under the strong pull necessary to raise the long column. Experimentation appears to bear out these requirements. The osmotic pressures maintained in the living cells within the leaf are sufficient to draw water from the xylem elements of the veins and thus raise a water column of a height equal to that of the tallest trees. There seems also to be little doubt that the cohesion of water contained within narrow tubes of cellulose is sufficient to transmit the tension (pull) throughout the whole column without its breaking. The cross walls in the tracheal tubes and the end walls of the tracheids do not interrupt the columns for these walls are saturated with water. It has been pointed out that bubbles are of frequent occurrence in the conducting elements of the xylem but it does not follow that these bubbles break the continuity of the water column. Such a bubble might expand until it completely filled the tracheid or compartment of a tracheal tube in which it originated. Further it could not go because of the immense force necessary to draw gases not in solution, through wet cell walls.

The tracheid or tracheal tube compartment containing the bubble might become inoperative in water conduction but the upward stream would flow around it through unobstructed wood elements.

The principal factors, then, in this theory are as follows: (1) The maintenance of high osmotic pressures in the mesophyll cells of the leaf, as a result of transpiration from these cells; (2) withdrawal of water from the tracheal tubes and tracheids; (3) the presence of continuous columns of water, extending from the leaves to the roots, and capable of holding together by means of their own cohesive force.

It is very likely that under normal conditions it is evaporation from the leaf into the relatively dry surrounding air which maintains the high concentration of the living cells within the leaf and causes the rise of the transpiration stream. However, it has been demonstrated that the upward flow of the transpiration stream does not cease if the leaves are surrounded by a saturated atmosphere or even if they are immersed in water. If the lower end of a leafy stem be placed in a solution of the red dye, eosin, the colored solution will rise in the wood, though quite slowly, even if the leaves are surrounded by water-saturated air or submerged in water. Accordingly, we must assume that the living cells of the leaf can actively secrete water when normal transpiration is prevented and thus keep up a high cell sap concentration and maintain the upward movement of sap in the xylem. Whereas ordinary transpiration probably does not involve any expenditure of energy by the leaf such active water loss into water-saturated air or water surrounding the leaf would necessitate the leaf using energy.

Conduction of Food.—As already stated, there is evidence that conduction of foods, including soluble carbohydrates, proteins, and amino acids takes place chiefly in the phloem. The amino-acids are the relatively simple, and soluble and diffusible nitrogenous compounds out of which proteins, which are mostly not truly soluble or easily diffusible, are built up. It is known that a complete girdling or ringing of the trunk of a tree, that is, the removal of a band of bark down to the xylem finally results in the death of the plant through starvation of the roots. If outer portions only of the bark are removed and the phloem is left intact, the roots do not suffer and there appears to be no marked interference with food conduction. Furthermore, chemical tests show that various foods are present in larger quantities in the sieve tubes than would be likely if they did not serve for food storage or transfer. Some of this food is in the form of small particles or in the colloidal condition, in which it cannot pass readily through cell walls or cytoplasmic membranes. The openings through the sieve plates (end walls of the sieve-tube elements) and the resulting continuity of the pro-

toplasm throughout long rows of sieve tubes permit movement of such foods through the sieve tubes without obstruction by cell walls or cytoplasmic membranes. In the spring, when active growth is renewed, food may move upward from points of storage in roots and stems to the buds. Then and perhaps for short distances at other times there may be some upward movement of food in the xylem.

Although the sieve tubes are undoubtedly the principal food-conducting elements of the phloem, phloem parenchyma may also convey carbohydrates and amino-acids longitudinally. Foods pass transversely in the stem along the vascular rays. Conducting elements of both xylem and phloem come in contact with vascular ray cells. Where the vascular ray cells adjoin these conducting elements there are pits which facilitate passage of materials to and from the ray cells (Fig. 77). Thus the vascular rays are able to carry food from the sieve tubes and phloem parenchyma radially into the xylem where it may be used to thicken the walls of developing tracheids and vessels and to supply the needs of the living protoplasts of the wood parenchyma cells, or to the pith, where it may be stored.

FIG. 97.—A portion of a cross section of pear stem. The section was stained with iodine to show the location of starch. Note that starch occurs chiefly in the pith rays and the outer cells of the pith, which regions appear darker than the surrounding tissues. (After Gardner.)

Storage in Stems.—Various substances, such as water, food, and waste products, may accumulate in stems. These stored products may or may not be utilized later by the plant. The fleshy stems of such plants as cacti, *Begonia*, glasswort (*Salicornia*), purslane (*Portulaca*), and various spurges (*Euphorbia*) accumulate large quantities of water. The water storage tissue usually consists of large thin-walled cells in the cortex or pith.

Stems may also serve as storage places for food. The chief storage tissues are vascular rays, wood parenchyma, endodermis, phloem parenchyma, cortex, and pith (Fig. 97). Starch is the most common form of stored food in stems. For example, in young apple twigs starch is abundant in the pith, especially near the nodes. Cane sugar (sucrose), reserve fats and proteins are also present.

It has been recently asserted that, in the case of certain trees, at least, the carbohydrates stored in the roots are used by the roots and are not transferred to the stems or leaves. Furthermore, it seems likely that the activity of the cambium cells depends upon stores of carbohydrates in the endodermis and in vascular rays; and that bud development in the spring is made at the expense of carbohydrates stored near the bud.

Subterranean stems, such as tubers, rhizomes, and corms, are especially adapted for food storage. Starch is the chief storage product in such structures. The starch is formed in the storage cells when surplus sugar (probably glucose) reaches these cells from the leaves. The change from glucose to starch takes place within leucoplasts of the storage cells. This change is a chemical condensation, many molecules of glucose ($C_6H_{12}O_6$) each losing a molecule of water unite to form a starch molecule $(C_6H_{10}O_5)_n$. The letter " n " indicates our uncertainty as to how many glucose molecules go to make up a single starch molecule. Before this reserve carbohydrate can leave these storage organs to be used elsewhere in the plant it must be digested, by hydrolysis, to form sugars again. This process of hydrolysis involves the taking up of water and the breaking down of the large starch molecule into molecules of simple sugars. It is the reverse of condensation. Condensation of amino acids to proteins also takes place in plants and is comparable to the condensation of simple sugars to form starch. Insoluble or colloidal proteins may also be digested to simpler nitrogenous compounds or even to amino acids by hydrolysis. Such condensation and hydrolysis of carbohydrates and nitrogenous food materials are brought about in plants and animals by the presence of certain enzymes.

The stems of some plants accumulate such substances as mucilage, resins, essential oils, tannins, and latex. In many ferns there are special

ducts which secrete a mucilaginous substance. Most conifers possess **resin ducts** (Fig. 98). Also, in certain composites, the rosin-weed (*Silphium*), for example, resin or oil ducts are abundant in the stems. **Tannins** are found in the stems of many plants. They are particularly abundant in the bark of tan oaks, and in the heartwood of many trees. **Latex** is a milky secretion formed in the highly branched system of tubes extending throughout certain plants (Fig. 99). These latex tubes have no cross walls and are distinct from the vascular system. Latex occurs in many different plant families. Common latex plants are the fig (*Ficus*), dandelion (*Taraxacum*), spurge (*Euphorbia*), and milkweed (*Asclepias*). The latex of plants is a very complex mixture containing such materials as sugar, oil, starch, protein, alkaloids, tannins, gums, resins, and salts of magnesium and calcium. Some regard

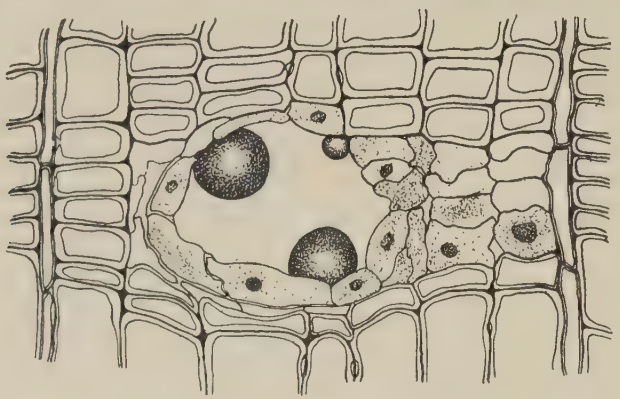


Fig. 98.—Resin canal as seen in cross section of wood of *Pinus strobus*. Observe the globules of resin in the canal.

latex tubes as food-storage organs; others consider that they are reservoirs of waste materials; still others regard them as serving for the storage of both waste products and reserve foods. The very important part which rubber plays in modern commerce, particularly in connection with the electrical and automobile industries, has directed a great deal of attention to latex and latex producing plants, for the latex is the principal raw material of rubber. The most important rubber-producing species is *Hevea brasiliensis* but a number of other members of the spurge family (Euphorbiaceae) and *Ficus elastica* and other plants of the fig family (Moraceae) are of some importance as rubber sources.

Propagation by Means of Stems.—It is a familiar fact that many plants may be propagated (multiplied) by means of stem pieces. For example, in the commercial propagation of such plants as roses, carna-

tions, chrysanthemums, sugar cane, fig, grape, and many other plants, this method is much used. When these cuttings are placed in moist soil, roots develop at the lower end, and one or more axillary buds develop into leafy shoots. Thus, each cutting grows into an independent plant. Under natural conditions, pieces of the stem may become detached and develop in the same way into new plants. Propagation by means of cuttings, whether of stems or of other vegetative structures, is of great importance in agriculture, because by this method new plants may be secured which are true to type. It is a matter of common knowledge that in the propagation of many economic plants by means of seeds the offspring are often quite unlike the parent. Strawberries, for example, seldom come true to type when grown from seed. Hence, it is possible to secure new varieties by planting seed, but when a desirable variation appears it is propagated by means of plants which develop at the nodes of runners, and thereby kept true. Propagation by means of cuttings of stems, roots or leaves, or by grafting often has the additional advantage that the cuttings or grafts develop more rapidly than plants grown from seeds.

FIG. 99.—Latex tubes in the root of dandelion (*Taraxacum taraxacum*). (From Winton, after Tschirch.)

Propagation by grafting is a very old horticultural practice, and is in common use in propagating fruit trees. In grafting, a piece of one stem, called the **scion,** is attached to another stem, which is rooted and is called the **stock,** in such a way as to bring together the cambium layers of each (Fig. 100). When a stem is wounded, as in grafting, by a cut that involves the cambium, the cambium is stimulated to active growth and forms a mass of large, thin-walled cells known as **callus.** While the callus is in the process of formation, a new cambium is formed by differentiation of inner callus cells, and this cambium becomes continuous with the cambium of stock and scion. Phloem and xylem elements are then formed which link up phloem and xylem of scion and stock. Thus there is a union of the stock and scion. At the same time, cork cells are differentiated from outer cells of the callus, and

these become continuous with old cork and thus effectively close over the point of union of scion and stock.

Budding is a horticultural practice which is essentially the same as grafting. It differs from grafting only in the character of the scion. In budding, the scion used is a single bud together with a small strip of adjoining bark. This is attached to the cut surface of the stock in such a manner as to bring the cambium of stock and scion together. The process of healing and union is similar to that which takes place in the case of a graft.

FIG. 100.—Stem grafting. Two scions are shown in center; at left, the scions are inserted in clefts of the stock, and in such a manner as to bring the cambium tissue of stock and scion in close contact; at right, the grafts have been waxed over, and covered with cloth. (From the Division of Pomology, College of Agriculture, University of California.)

Growth Medium of Stems.—The growth medium of stems may be either air, soil, or water. Many plants produce both aerial and subterranean stems. For example, asparagus, rhubarb, and Irish potatoes have underground stems, and from these are sent up aerial stems bearing foliage leaves and flowers. Water also is in some cases the medium of growth of stems, as in such plants as *Elodea*, *Potamogeton* and various water lilies, etc. Such aquatic stems possess extensive systems of large connecting air spaces in the tissue of the stem in which air is stored. The

entire stem system of most plants grows in air. In our common ferns the entire stem is underground but in the tropical tree ferns there is an erect aerial stem or trunk bearing a leafy crown.

STEM MODIFICATIONS

Ordinarily we think of a stem as a cylindrical organ growing more or less erect, but there are many modifications of stems differing so much in form and in other respects from the ordinary type that they are scarcely recognizable as stems, and careful study of their origin and structure is often necessary to identify them as such. We shall discuss briefly the following types: rhizome, tuber, corm and runner, all of which are vegetative reproductive structures.

Fig. 101.—Iris plants, showing the rhizomes with leafy shoots and roots. (From Bocquillon.)

Rhizomes. — These are elongated, underground, horizontal stems, generally rich in stored food. The rhizomes of Canada thistle (*Carduus arvensis*), Johnsongrass (*Sorghum halepense*), quackgrass (*Agropyron repens*) *Iris*, (Fig. 101), and many ferns are good examples. Rhizomes bear reduced scale leaves at the nodes. Rhizomes, like typical aerial branches, possess terminal buds and produce lateral buds at the nodes in the axils of the leaves. The lateral buds may give rise to aerial stems which usually die back to the ground each autumn.

Rhizomes generally produce large numbers of adventitious roots. Many of our most pernicious weeds are rhizome-bearing perennials. Familiar examples are wild morning glory (*Convolvulus*), Canada thistle (*Carduus arvensis*), quackgrass (*Agropyron repens*), Johnsongrass (*Sorghum halepense*), nutgrass (*Cyperus rotundus*) and poverty weed (*Iva axillaris*). In the eradication of weeds of this class it is not suf-

ficient to merely prevent the maturing and spreading of seed, for the plant is capable of propagating itself readily by means of the rhizomes, as well as by means of seeds. If the aerial stems are cut to the ground line, new shoots are promptly sent up from the subterranean stems

FIG. 102.—Quackgrass (*Agropyron repens*) showing the underground horizontal stems (rhizomes) and the general habit of plant.

(rhizomes). Furthermore, if the rhizomes are broken into a number of separate pieces by cultivating implements, each piece may grow. This is simply a case of propagation by cuttings. Frequent cultivation, having as its aim the destruction of new shoots as soon as they appear,

may succeed in starving out the rhizome after a time, since food is made only in the green parts of the plant. When the food-making organs are removed, a certain amount of the reserve food in the rhizome is drawn upon to produce new aerial shoots. If these are again cut off as soon as they appear above ground, and before they have an opportunity to manufacture food, the rhizome will finally become exhausted by the successive drains on its reserve.

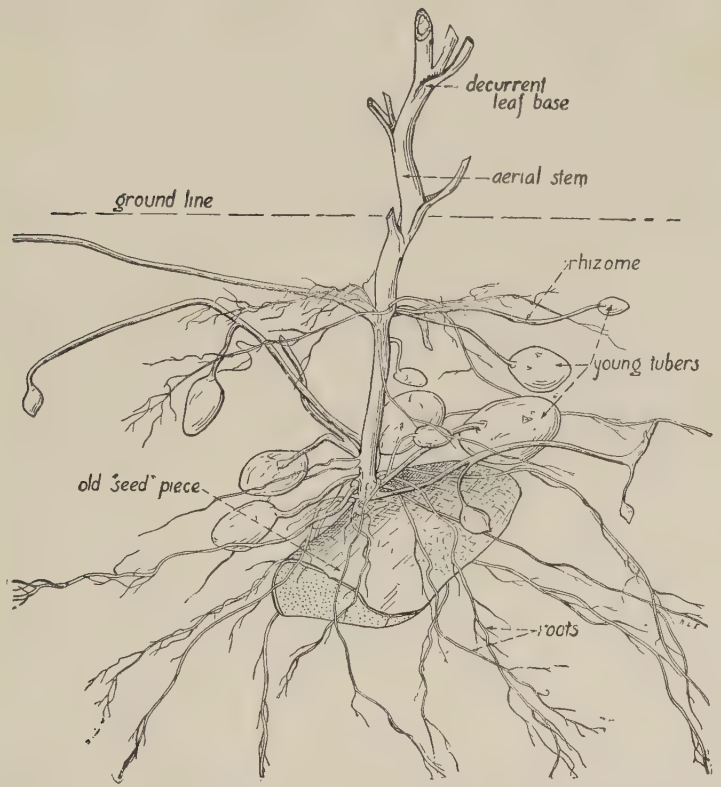


FIG. 103.—Portion of a sprouting potato tuber. (After Robbins, *Botany of Crop Plants.*)

Tuber.—A tuber is a much enlarged, short, fleshy underground stem. Tubers differ from rhizomes in their stouter form, their generally shorter internodes and the usual absence of roots. They are commonly produced at the ends of rhizomes. The most familiar example of a tuber is the common Irish potato (*Solanum tuberosum*). When a piece of a potato tuber (really a stem cutting) is planted, "sprouts" are sent out from the "eyes." From these sprouts arise branches,

some of which run horizontally underground (Fig. 103). These horizontal structures have nodes and internodes and scale leaves and are quite obviously rhizomes. Soon, the tip of a rhizome begins to enlarge and a potato tuber is formed. Furthermore, examination of the potato reveals the presence of a terminal bud at the " seed end " of the tuber, groups of lateral buds (" eyes ") along the sides, and near each " eye " a small scale leaf. In an elongated potato, we may be able to make out the spiral arrangement of the buds, due to the fact that there is only one bud at a node. Lenticels may also be observed on the corky layer (skin) of the potato.

Careful study of a cross section of a potato tuber reveals the following regions:

1. Periderm or " skin," consisting of cork and cork cambium.
2. Cortex from which the pericycle is not distinguishable.
3. Ring of vascular bundle.
4. External medulla or pith.
5. Internal medulla or pith.

The original true epidermis gradually dies and sloughs off, and the outer corky layer of cells constitutes the periderm or skin of the potato.

The vascular bundles form a discontinuous ring. At the eyes, the vascular tissue approaches the surface of the tuber and bundles branch out into the buds which usually occur in groups, each group lying in a more or less depressed area. Such a group of buds is called an " eye." The depression is the axil of a scaly leaf which is in evidence when the tuber is young, but later disappears. Actually the eye is a lateral branch with undeveloped internodes, the whole tuber being generally a much-branched stem and not a simple shoot. The central (terminal) bud in the " eye " is commonly the largest and most vigorous.

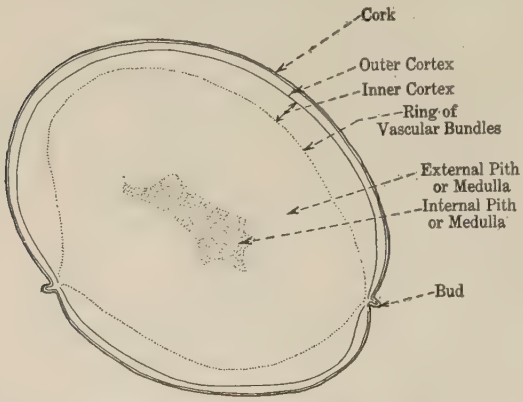


FIG. 104.—Diagram of potato tuber as seen in cross section.

Bulb.—A bulb consists of a short, flattened or disc-shaped underground stem, from which arise numerous fleshy scale leaves filled with stored food. Actually a very small proportion of the tissue in a bulb is

stem tissue and a bulb is rather a modified shoot than a modified stem. The common onion (*Allium cepa*) is a typical example of a bulb (Fig. 105). When an onion bulb is cut lengthwise through the center, one can see a small disc-shaped stem upon which are borne the numerous scale leaves which completely encircle the terminal bud at the tip of the stem. Lateral buds may occasionally be found in the axils of the scale leaves. In the lower part of the disc-like stem there are many rudimentary adventitious roots which develop when sufficient moisture is available. The terminal bud develops into the aerial shoot of the plant and the axillary buds into new bulbs. The reserve carbohydrate of most bulbs is not starch but sugars.

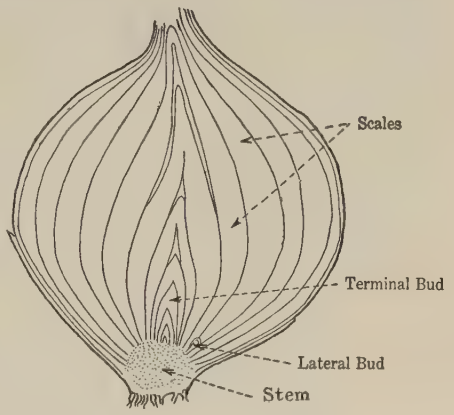


FIG. 105.—Median longitudinal section of an onion bulb.

Corm.—A corm is a short, solid, vertical, enlarged underground stem in which food is stored. A common example of a corm is the underground stem of gladiolus or crocus (Fig. 106). Corms are usually flattened from top to bottom, and bear a cluster of thick fibrous roots at the lower side, and a tuft of leaves on the upper side. They differ from bulbs principally in being almost entirely made up of stem tissue with relatively few scale leaves whereas a bulb consists mostly of fleshy scales.

FIG. 106.—Corm of crocus, in median longitudinal section. (Redrawn from Figurier.)

Runner.—A runner, or stolon, is a stem that grows horizontally along the surface of the ground. It resembles the rhizome in that its direction of growth is more or less horizontal, but differs from the rhizome in not being underground. The runners of the strawberry plant (Fig. 107) arise as axillary branches. The runners

have long internodes, and produce leaves, flowers, and roots at certain nodes. Examination of runners shows that, whereas there are scale leaves at every node, new shoots and roots develop only at every other node. That is, between the parent plant and the first daughter plant, there are two internodes, between the latter and the second daughter plant, two internodes, and so on. Finally, the terminal bud develops a new plant. By the death of runners, daughter plants become segregated from their mothers.

Stem Tendrils.—Although tendrils are generally formed from some part of the leaf, there are tendrils which are morphologically stems.

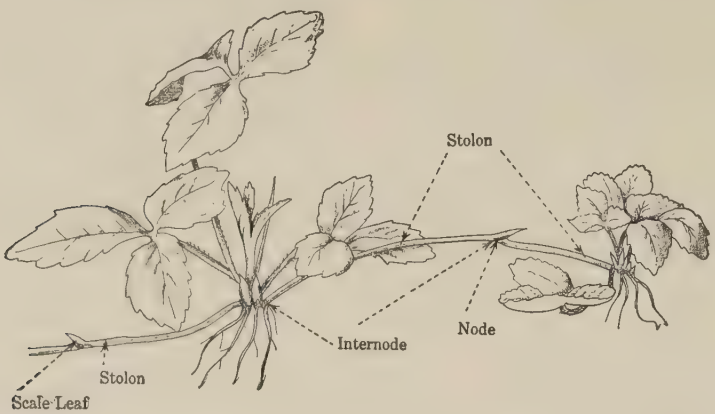


FIG. 107.—A strawberry (*Fragaria*) plant showing propagation by means of stolons.

This is shown by the fact that they may arise in leaf axils and bear small leaves or flowers. In the Fox grape (*Vitis*) the tendrils are stem tendrils; there is either a tendril or an inflorescence opposite each leaf.

OTHER MODIFIED STEMS

Stems may be modified to serve many other functions than those which have been mentioned above. Thus the spines of the honey locust (*Gleditsia*), *Colletia cruciata*, and a number of other plants are modified lateral branches. Not all spines or prickles are stem structures, however. Some are outgrowths of the epidermis (spines of roses) and others are modified leaves or leaf parts while in a few cases roots become modified into spines.

A good many xerophytic plants (plants of very dry habitats) are leafless, or produce leaves which are shed very soon after their appear-

ance so that they are bare most of the year. This is generally interpreted as an adaptation to the environment since the reduction of surface through loss of leaves presumably lessens the danger of excessive water loss. However, that may be, such plants must carry on assimila-

FIG. 108.—Two branches of *Colletia cruciata*, a xerophytic plant in which green, flattened lateral branches serve as photosynthetic organs and also as spines. The branch to the right is taken from an actively growing branch and shows the small temporary leaves. The branch to the left shows the characteristic spiny branches and in several places the scars of the leaves in the axils of which the branches had their origin as axillary buds.

tion and in the absence of leaves, this function is performed by the stems, which are often flattened and somewhat leaf-like in form. The lateral branches of *Colletia cruciata* serve not only as spines but also are flattened and take the place of leaves in photosynthesis. Other

examples are certain species of *Ruscus*, *Muehlenbeckia platyphylla*, and various species of the cactus (*Opuntia*). Such flattened, green

FIG. 109.—Species of *Echinocactus*, showing fleshy storage type of stem. (From Willis T. Lee in The National Geographic Magazine.)

stems of leafless plants are called *cladodes*. They may bear flowers, fruit, and temporary leaves.

CHAPTER V

THE ROOT

Introduction.—As already stated in the chapter on The Plant Body, the plant body of most spermatophytes or seed plants is made up of shoot and root, the former consisting of stems and leaves. In that chapter (see page 19) the distinctions between stems and roots, which may in some cases bear strong superficial resemblances, were discussed. Briefly summarized these distinctions are;

ROOTS	STEMS
1. Roots rarely grow upward.	1. Stems rarely grow downward.
2. Roots are not divided into regions (like nodes of stems) from which branches may arise, alternating with regions from which branches do not arise.	2. Stems are made up of alternating nodes (from which leaves and branches may arise) and internodes, which are leafless and without branches.
3. The branches of roots originate within the root from which they arise.	3. Branch stems originate at the surface of the stems from which they arise.
4. The growing point of the root is covered by a special protective structure, the root cap.	4. The growing point of the stem is not protected by any special structure but by rudimentary foliage leaves and frequently by bud scales (modified leaves) also.

In addition to these points of difference, roots and stems differ very greatly in the arrangement of their primary tissues. Those roots which, however, develop cambium and thus grow in thickness come to resemble old woody stems in their anatomy.

Kinds of Roots.—According to their origin, roots may be classified as **primary roots, secondary roots** and **adventitious roots.**

The primary root of a plant is the root which develops from the radicle (rudimentary root) of the embryo of the seed from which the plant grew. It is the first root of the plant and in many species remains the principal root throughout the life of the plant.

Branches of the primary root are called secondary roots. It is sometimes convenient to distinguish branch roots of the second order, that is branches which arise from secondary roots, as tertiary roots.

We shall, however, use the term secondary roots to include all branches of primary roots of whatever order.

All roots arising anywhere except from the radicle or as branches of the primary root are spoken of as adventitious roots. Adventitious roots may arise on stems and even in some cases (*Begonia, Gloxinia* and *Bryophyllum*) from leaves. The prop roots of corn (*Zea*) which grow out from the lower nodes of the stem and, entering the soil obliquely, serve as braces for the plant, are good examples of adventitious roots. The roots which grow out from planted tubers, bulbs and rhizomes are adventitious roots and when stem cuttings of such plants as pear (*Pyrus*), blackberry (*Rubus*), geranium (*Pelargonium*) and rose (*Rosa*) are placed in damp sand or soil, there will be produced at the lower end a number of adventitious roots. From these the root system characteristic of the plant will be developed.

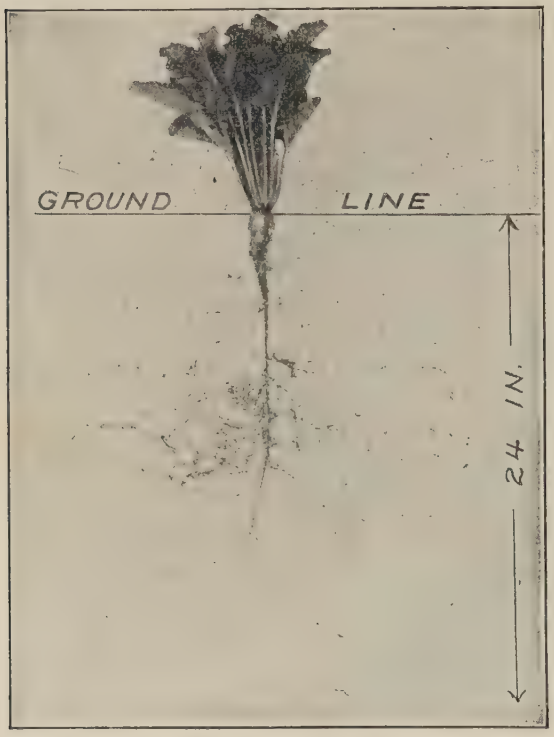


FIG. 110. -Young sugar beet (*Beta vulgaris*) plant showing the root system. (After Robbins, *Botany of Crop Plants.*)

Kinds of Root Systems.—In many species of plants, especially among the monocotyledons, the primary root does not become the principal root of the plant but may stop growing while the plant is still young. In such cases the functions of anchorage and absorption are taken over by numerous adventitious roots which grow out at the base of the stem. There results what is spoken of as a **fibrous root system,** which is characteristic of corn (*Zea*), wheat (*Triticum*), and other grasses, the palms and many other kinds of plants.

When the root system consists principally of an actively growing primary root with its branches (secondary roots) it is spoken of as

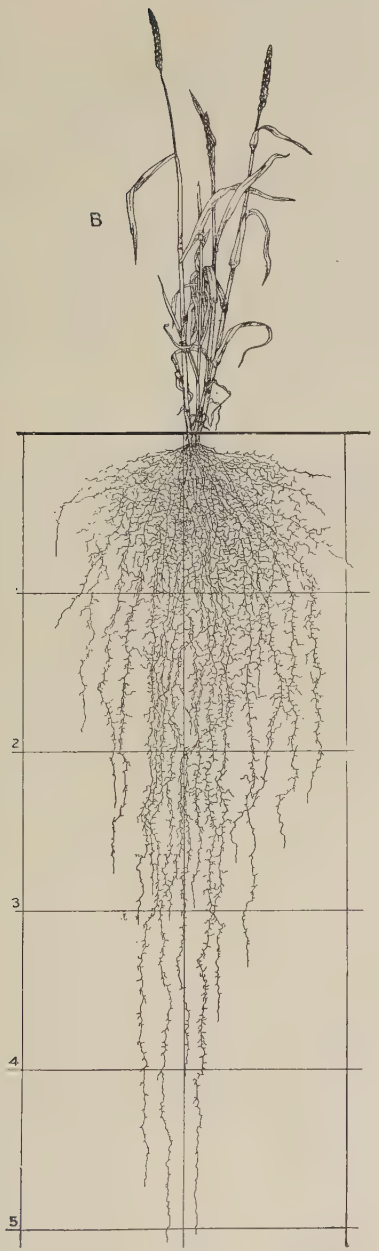


FIG. 111.—Fibrous root system of wheat. The numbers indicate depth in feet. (After Weaver, Carnegie Institution of Washington, Pub. No. 316.)

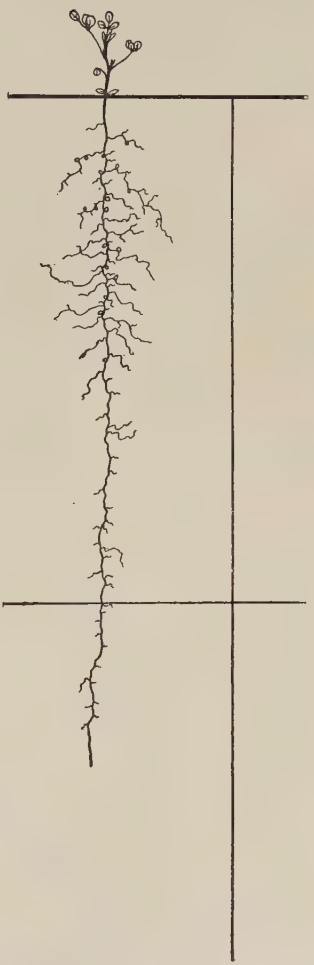


FIG. 112.—Tap root system of young sweet clover plant (*Melilotus*). (After Weaver, Carnegie Institution of Washington, Pub. No. 316.)

a **tap root system** or **primary root system.** Most conspicuous among the many examples of plants having such a root system are the carrot (*Daucus*), beet (*Beta*), radish (*Raphanus*), turnip (*Brassica*), and parsnip (*Pastinaca*) and other such plants in which the primary root is greatly enlarged for food storage. In most cases, as in dandelion (*Taraxacum*), and oak (*Quercus*) the primary or tap root is not so conspicuously enlarged.

The Form of the Root System. —Just as we recognize great differences in the form of the shoot systems of our common plants, so do

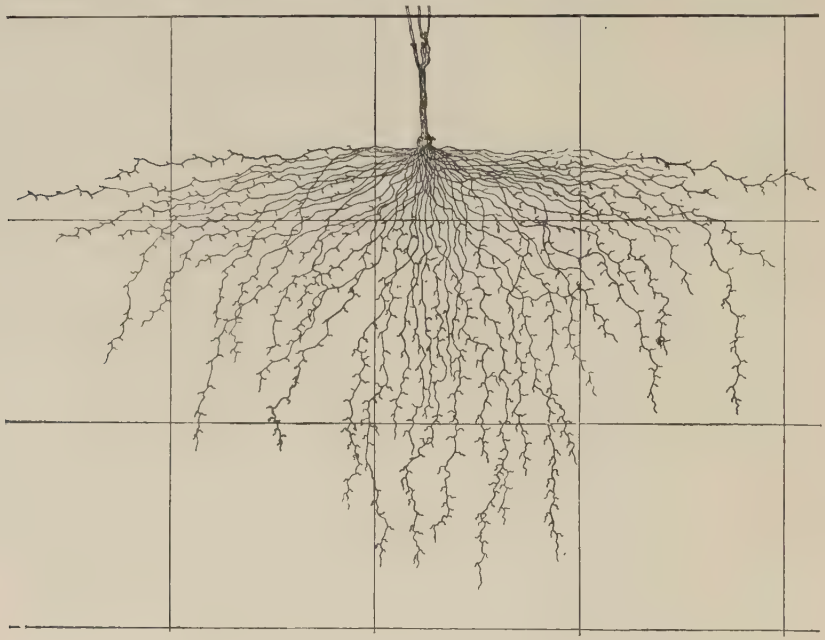


FIG. 113.—Corm and root system of blazing star (*Liatris*). (After Weaver, Carnegie Institution of Washington, Pub. No. 292.)

we find conspicuous differences in the form of root systems. For obvious reasons, we are much more familiar with the form of the shoot system, which grows in the air, than we are with the form of the root system, which is in the soil.

Figures 111, 112 and 113 illustrate various types of root systems. Although soil conditions exert a marked influence on the form of the root system, it is, to a considerable degree, a specific characteristic of the plant, just as is, for example, the form of the crown of a tree. The cereals and most grasses have shallow root systems which in general assume a broad, pyramidal form, the apex of the pyramid being at the

ground line. The sugar beet (*Beet vulgaris*) has a deep root system, the general form of which is rectangular.

Though shallow root systems are characteristic of certain species of plants and deep root systems of others, the depth of the root system in many cases varies greatly with soil conditions. Plants living in a dry region where they must depend for water mostly on occasional showers profit by a shallow root system with great numbers of roots in the first few inches of soil beyond which the water seldom penetrates. On the other hand, for plants growing in regions where they must depend principally on water deeper in the soil, the deep root system is more advantageous. As far as firm anchorage of the plant is concerned the deep root system is obviously more efficient than the shallow.

STRUCTURE OF ROOTS

External Features.—The root is an almost cylindrical structure, very gradually tapering from its base, where it is attached to the stem or a larger root, toward its free end or **root tip.** It is in the four to six centimeters of the free end that growth in length, water absorption and most of the primary development of the tissues take place. This part of the root may for convenience in describing it be divided into the following regions beginning at the very end:

The root cap
The growing point
The region of elongation
The region of root hairs.

The root cap is a protective structure consisting of a thimble-shaped mass of cells covering the end of the growing point. It will be recalled that in the case of the stem the growing point is protected by the rudimentary leaves and scales of the bud. Protection of growing points may be necessary (1) because of the thinness of the walls of the promeristem cells which makes them particularly liable to mechanical injury and drying out and (2) because these cells upon which the growth of the organ depends, are of such great importance to the plant. In the case of the root, protection of the growing point from injury through an excessive loss of water is generally not necessary since the root tip is seldom exposed to dry air. Danger of mechanical injury, is, however, much greater than in the case of the growing point of the stem, for the tip is constantly being forced through the soil which is largely composed of pieces of rock. By reason of this abrasion of the cap by the soil particles it is continually being worn away but at the same time new cells are being added to it where it is in contact with the growing point.

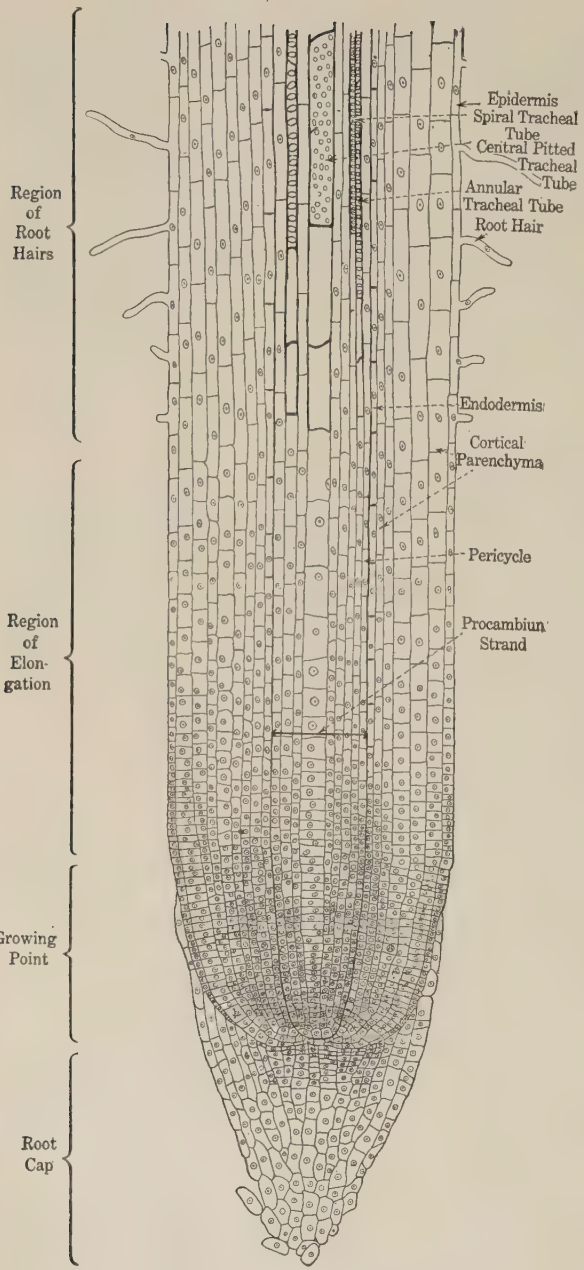


FIG. 114.—Longitudinal section of the root of barley (*Hordeum sativum*).

The passage of the root tip through the soil is facilitated by the fact that the outer layers of cells of the root cap become mucilaginous and thus render the cap rather slimy.

The **growing point,** as in the stem, consists of tissue (promeristem) in which active cell division is going on as long as the root is growing. This region of the root is in most cases about a millimeter in length. Growth in length takes place in this region but at a very much slower rate than in the **region of elongation** just behind it. As the result of active cell division, the number of cells in the growing point tends to increase. We have seen that some of these cells are added to the root cap. Others are constantly passing over into the region of elongation.

In the **region of elongation** the cells produced in the growing point undergo very rapid growth in length as the result of the absorption of large quantities of water and the stretching due to the high

turgor thus developed. This region of the root is generally from two to five millimeters long.

In the **region of root hairs,** elongation has ceased and the surface of the root becomes clothed with a dense growth of root hairs, which are tubular outgrowths of the epidermal cells and which are closed at the free ends. These structures are not only of great importance particularly in connection with the absorptive function of the root but also in anchoring the roots firmly in the soil. In the case of pea (*Pisum*),

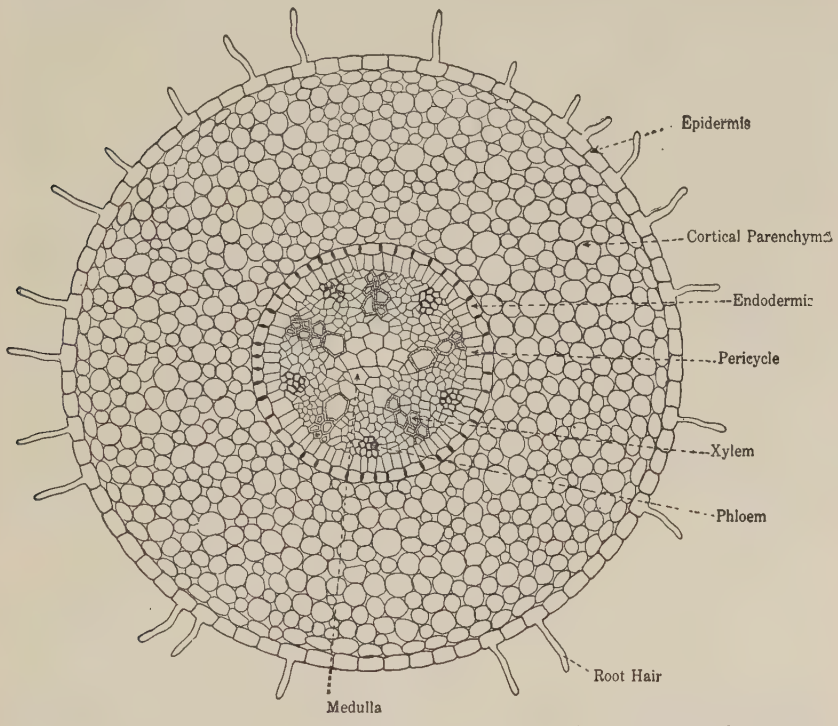


FIG. 115.—Cross section (diagrammatic) of a young dicotyledonous root through the root-hair zone.

there may be 230 and in corn (*Zea mays*) as many as 420 hairs per square millimeter. It is in this zone that the cells inside the root, which were produced in the growing point and which increased greatly in length in the region of elongation, differentiate into tracheal tubes, tracheids, sieve tubes, and the various other permanent tissues of the root. On this account it might be spoken of as the **region of maturation.**

These four regions which have been briefly described are spoken of together as the **root tip.** In the part of the root behind the tip the root hairs are withered and dead, for the life of each root hair is but a

few days, the older ones dying off as new ones are produced at the lower end of the root-hair zone. In the older part of the root, growth in length never takes place but there is sometimes an actual shortening. It is in this region that secondary roots make their appearance. In many dicotyledons and in most gymnosperms there is later secondary growth in thickness with the formation of a large central cylinder of wood and a covering of cork tissue, but these changes belong rather to the discussion of the anatomy of the root.

Anatomy of the Root.—Roots are much more uniform in their internal structure than are stems and we shall not have to study several types as we did in the case of stems. It will be easier to gain an understanding of the anatomy of the root if we consider in order a series of cross sections from the growing point to the mature region of the root, a method similar to that used in describing the development of the stem tissues.

A Cross Section Through the Root at the Growing Point.—A section across the root through the growing point shows a disc of tissues made up of typical meristematic cells, thin walled, all very much alike, practically without intercellular spaces. If the section is made at one of those times during the day when nuclear division is most active, a great many nuclei will be in some stage of mitosis. The resting nuclei will be found to be much larger in proportion to the size of the cells than in permanent tissues. Outside of the tissues (promeristem) of the growing point there will be found in such a section a ring of cells which may be quite separated from the tissue of the growing point. These are cells of the root cap where it extends back over the growing point.

A Cross Section Through the Region of Elongation.—This is also, of course, circular in outline. The cells in such a section are not uniform in appearance but some differentiation has taken place though the cells are still meristematic. A single layer of surface cells is the **protoderm.** A circular group of cells in the center of the section is the **procambium** and between this and the protoderm is the **ground meristem.** It will be recalled from the discussion of the anatomy of the stem that these three meristematic regions are spoken of as the primary meristems.

A Cross Section Through the Region of Root Hairs.—In this section the following primary permanent tissues can be seen:

1. The **epidermis** (derived from the protoderm) with its root hairs.
2. The **cortex** (derived from the ground meristem), the innermost layer of which is the **endodermis.**
3. The **stele** consisting of:

The **pericycle,** which is derived from the ground meristem, and the **xylem** and **phloem** derived from the procambium

The epidermis consists of a single layer of cells from which the root hairs arise. The cortex is composed of numerous layers of parenchyma cells and of a single innermost layer, the endodermis, the cells of which frequently have their inner and radial walls thickened. In other cases the endodermal cells have the walls thickened all around and in still others they are thin walled except for a portion of the radial walls. The thickened portions of the walls are cutinized and suberized.

The stele in the roots of almost all plants is a protostele, whereas, the stems of most seed plants have siphonosteles or dictyosteles. The

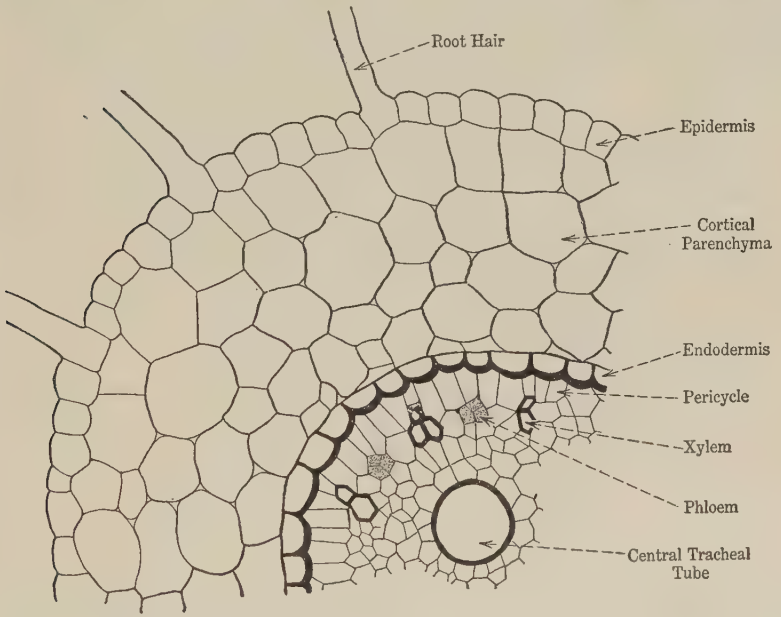


FIG. 116.—Cross section of the root of barley (*Hordeum sativum*), through the root-hair zone. (Redrawn from Percival.)

pericycle is the outermost tissue of the stele. It consists of from one to several layers of parenchymatous cells and generally is a continuous ring of tissues.

The arrangement of the vascular tissues is of the radial type (Fig. 115). The xylem elements are in groups which radiate from the center of the root and alternate with groups of phloem elements which lie in the angles formed by the radiating xylem groups. Xylem and phloem groups are separated by one or more layers of parenchyma cells. Commonly the groups of xylem elements meet at the center of the root so that there is no pith, but in some cases, especially in the roots of monocot-

yledons, the central cells are parenchymatous and form a pith. For the most part the xylem and phloem elements are similar in structure and function to those of the stem. Spiral and annular tracheal tubes are relatively infrequent in the root. This seems to be correlated with the fact that the region of elongation in roots is very short compared with that in stems. It will be recalled that such xylem elements are found in the part of the xylem which is first formed, that is, formed while the region in which they are produced is still elongating.

Growth in Diameter of Root.—In most monocotyledons and many annual dicotyledons there is no secondary increase in thickness of the roots. In such plants sections through older parts of the root would be essentially like sections through the root-hair zone. In the

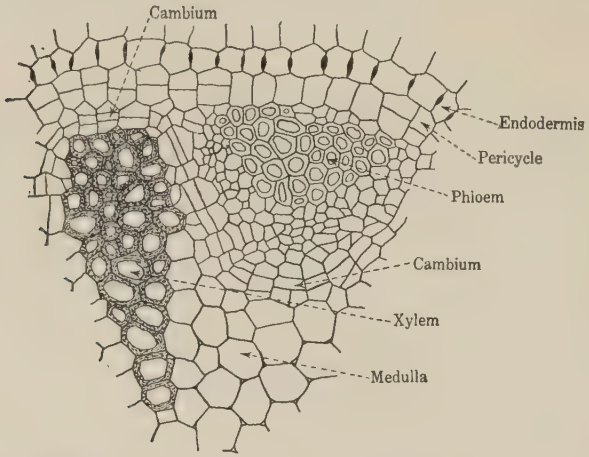


FIG. 117.—Cross section of a portion of the central cylinder of a primary root of horse-bean (*Vicia faba*), showing origin of cambium. (Redrawn from Haberlandt.)

region behind this zone the root hairs are withered and dead. The epidermal cells and frequently several adjacent layers of cortex cells become suberized and come to function as a protective layer.

In perennial dicotyledons and gymnosperm roots, a cambium arises and secondary increase in thickness normally occurs. Certain of the cells lying adjacent to the outside of the xylem and phloem strands, including those of the pericycle lying just outside of the xylem masses, become meristematic and form a cambium. At first, this vascular cambium, as seen in cross section, is not circular but has the form of a wavy band, since it passes inside of each phloem strand and outside of each xylem strand (Fig. 118).

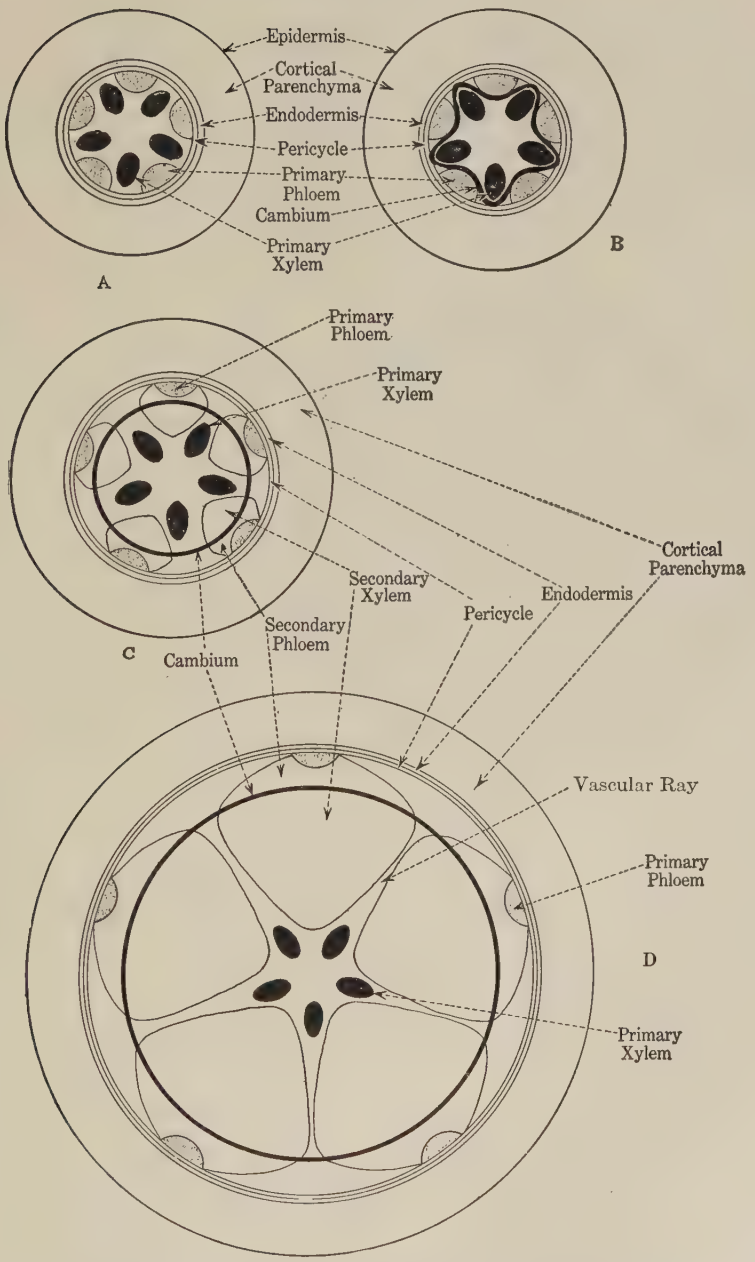


FIG. 118.—Diagrams showing stages in the secondary increase in thickness of a root. *A*, before the appearance of cambium. *B*, the formation of the cambium ring. *C* and *D*, stages in the development and growth of secondary phloem and xylem. Secondary increase in thickness due to the activity of phellogen is not shown.

Those portions of the cambium which adjoin the phloem give rise to new vascular elements both on the outside and on the inside. The new cells formed on the outer side become phloem elements, and are added to the phloem already present. Those formed on the inner side become xylem elements and thus new xylem strands are formed. There result at these points collateral vascular bundles similar to those in most stems. Where the cambium lies outside the original groups of xylem elements, it produces on both sides parenchymatous cells and thus forms pith rays which lie between the collateral vascular bundles. At the center of an old root the original radiating strands of xylem can usually be distinguished.

FIG. 119.—Transverse section of an old root of alder (*Alnus*). Note its resemblance in structure to an old stem. (After Jeffrey.)

Soon after the vascular cambium makes its appearance, certain cells of the pericycle undergo repeated division and thus form another cambium. This is called the **phellogen** or **cork cambium.** The cork cambium produces cork externally and secondary cortex internally. All the tissues which originally lay outside of the pericycle die soon after cork formation commences. As a result of the activities of these two cambiums, the old root comes to resemble in structure closely that of an old stem (Fig. 119).

In such fleshy roots as the sugar beet there are several zones or rings of vascular tissue, separated by broad bands of storage parenchyma. In the young seedling beet root, there is a central stele, surrounded by a narrow cortex, which is bounded by an epidermis. The stele consists of a central xylem plate, two phloem groups, a pericycle of one layer, and a mass of parenchyma tissue between the xylem and phloem The first or primary cambium arises in this parenchyma, except in the region opposite the two ends of the xylem plate where it originates from the pericycle. The primary cambium develops xylem and phloem in the normal manner, giving rise to the innermost circular layer. The first secondary cambium in the root is usually derived from parenchyma

cells of the primary phloem. Other supernumerary cambiums arise as follows: When the cells of the first secondary cambium cells divide, the outer daughter cell in each case becomes the initial cell of a new cambium, while the inner daughter cell divides further and produces xylem, phloem and medullary rays, and a broad band of storage parenchyma. This process is repeated until all the supernumerary cambiums have been formed one after another. A beet root the size of a pencil contains all the circular layers of the mature beet. The increase in the diameter of the beet is the result of cell division and enlargement going on at the same time in all the rings. As a rule, only the inner five or six rings mature their tissues.

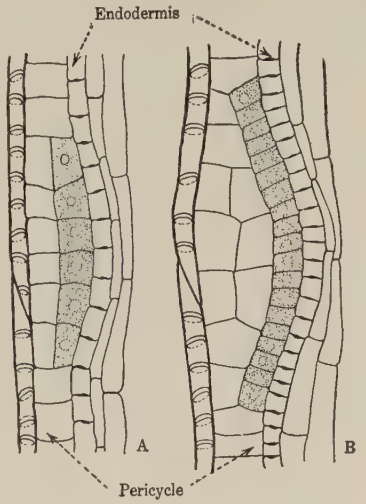


FIG. 120.—Two stages in the development of a branch root. Certain pericyclic cells (here stippled) become meristematic, first undergo tangential division, and thus initiate the process of branch root formation. (Redrawn from Van Tieghem.)

Root Branching.—It will be recalled that the outermost tissue of the stele is the pericycle. It is in this layer that branch roots have their origin. The first evidence of the formation of a branch root is the tangential division of certain pericycle cells (Fig. 120). Thus a group of meristematic cells is formed, and a root tip, with root cap, arises within the old root. The root tip must make its way outward through the cortex and the epidermis before reaching the surface. The growing point of the branch root is said to secrete enzymes which dissolve the cell walls of the tissues through which it is passing. Such branch roots do not emerge into the soil until elongation has ceased in that part of the main root from which they arise.

Root Hairs.—The importance of root hairs to the plant is so very great that it is desirable for us to learn more of their structure and functions. It is absolutely essential to the life of all typical land plants that they secure from the soil an amount of water at least equal to the quantity which they lose to the air by transpiration. If such a plant is to grow and develop normally, additional water is necessary for photosynthesis and to supply that required for the formation of new cells. Thus, one of the greatest problems of all seed-bearing plants, except aquatics, is to provide that water lost by the plant plus that used by it shall not exceed the quantity of water absorbed.

It is true that the roots are the absorbing organs, but water and soil solutes are not taken in at all points on the surfaces of the root system. We have already learned that the surface of old roots is covered with a layer of cork cells which is quite impermeable to water and mineral salts. Also, in old epidermal cells suberization greatly restricts the entrance of water and salts. On these accounts, absorption is carried on principally by root hairs and epidermal cells, which are found near the growing tips of the root. When we pull up a young herbaceous plant from loose soil, it is observed, as a rule, that it has a large number of hair-like rootlets, which are sometimes mistaken for root hairs. If these are examined with a hand lens it will be seen that these thread-like roots are covered at their tips with much smaller structures, the root hairs. That root hairs are the chief water-absorbing organs of a plant is indicated by the quick wilting of plants when many of their root hairs are destroyed. The root hairs are so tender and so closely attached to the soil particles that it is practically impossible to remove a plant from the soil without injuring or actually tearing off innumerable root hairs. Furthermore, a few seconds' exposure to dry air, such as often attends transplantation, is sufficient to shrivel the root hairs and to render them unable to perform their function. Consequently, the transplanted plant wilts and seldom revives until new root hairs are formed.

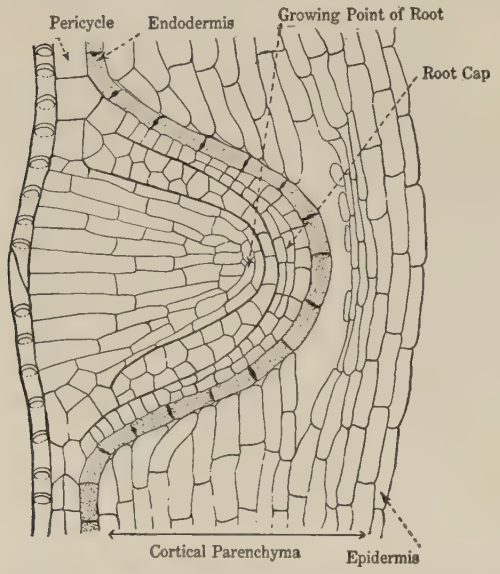


FIG. 121.—Later stage than shown in Fig. 120, showing the development of a branch root. (Redrawn from Van Tieghem.)

Structure of Root Hairs.—A root hair is a lateral protuberance of an epidermal cell (Fig. 126) having the form of a slender tube closed at the free end. A root hair and the epidermal cell from which it grows are not separated by a wall. They together constitute a single branched cell with a single protoplast. Though tending to cylindrical form, root hairs may become greatly contorted in their growth between and around soil particles. Root hairs vary in length from a fraction of a

millimeter to seven or eight millimeters. The walls are thin and of pure cellulose and are lined by a thin layer of cytoplasm so that the vacuole or vacuoles are relatively large. It should be specially emphasized that all the materials that enter the plant from the soil must pass through the walls of the root hairs or epidermal cells, and the cytoplasmic membrane within each. From the root hair, the absorbed materials are passed on to cells of the root cortex, to the pericycle and then into the conducting elements of the xylem. By these they are carried to various parts of the plant.

Root-hair Zone. — Functioning root hairs are not found along the full length of a root, but occupy a definite zone, known as the **root-hair zone.** This may be well observed in young seedlings grown in moist air. The root-hair zone appears as a white, fuzzy coating (Fig. 127). The root cap and growing point bear no root hairs. As we proceed backward from the growing point we perceive that the region of elongation is also devoid of root hairs, and that root hairs first occur just behind this region. This is clearly an advantage to the plant since it is obvious that if they were produced in the region of elongation, they would be broken off as the cells elongated. The length

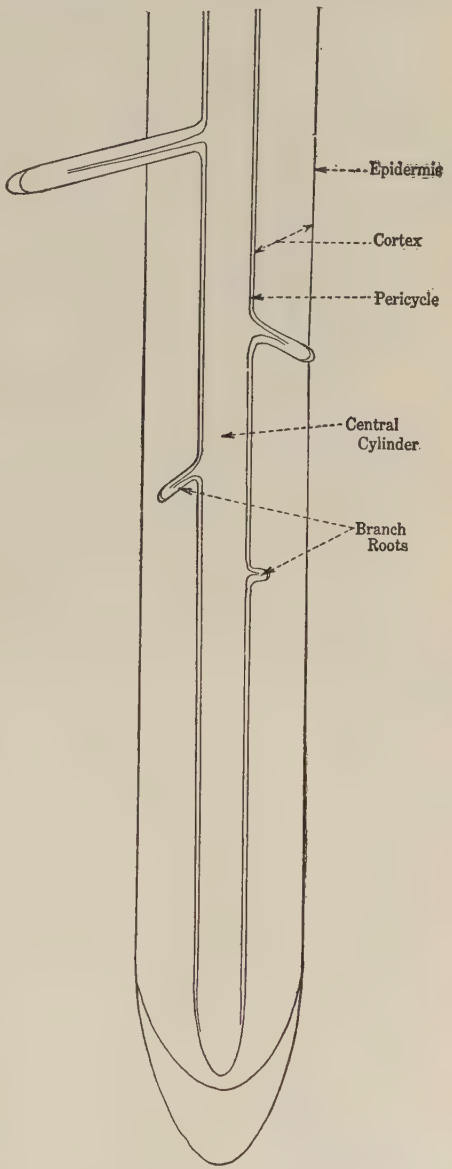


Fig. 122.—Diagram showing the manner of origin of branch roots.

FIG. 123.—Germinating seeds of garden cress (*Lepidium*) grown in moist air. Observe the dense white growths of root hairs.

of the root-hair zone varies from a few millimeters to several centimeters. If the roots of a plant growing in fine sand are removed from the soil, the root-hair zone is plainly evident because of the sand particles held by the root hairs (Fig. 124). Each root hair in its growth flattens out over, and sometimes partially surrounds, the soil particles with which it comes into contact (Fig. 125). Root hairs are short-lived, functioning for only a few days or weeks. New hairs are constantly formed at the root tip end of the root-hair zone, while the old hairs at the upper end of the root-hair zone are dying. The root-hair zone advances through the soil as the root grows. In this way root hairs are constantly brought

FIG. 124.—Wheat seedling showing soil particles clinging to the root hairs; note that the root tips are free of root hairs. (After Robbins, *Botany of Crop Plants.*)

into contact with new soil particles as new soil regions are invaded. This is of advantage to the plant, first because new stores of water and salts thus become available to the root hairs, and second, because these new soil regions are devoid of any deleterious substances which may accumulate in the neighborhood of the old hairs. These harmful substances, according to some, are excretions of the root hairs; according to others, they arise through the decay of root hairs themselves. There is some evidence that the deleterious substances which accumulate during the growth of a particular crop are more injurious to that crop than to another.

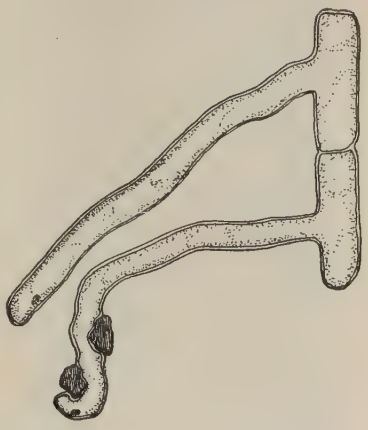


FIG. 125.—The relation of root hairs to soil particles. Root hairs in their growth may flatten out over, or partially surround, soil particles.

Many plants which produce root hairs when the root system grows in moist air or in soil, develop no root hairs when the roots are grown in water. A few aquatic angiosperms and several gymnosperms such as the firs (*Abies*) and *Pinus sylvestris* produce no root hairs.

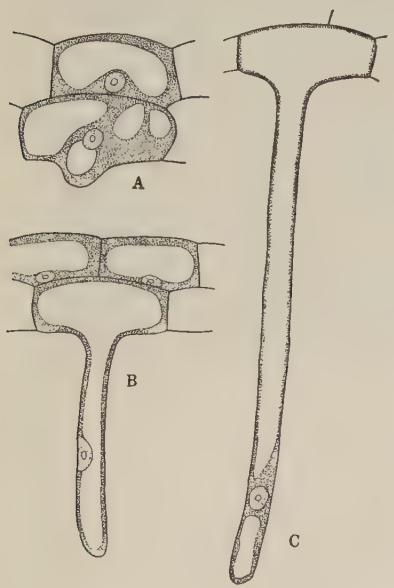


FIG. 126.—Stages in the development of a root hair. (After Frank.)

The Functions of Roots.—As was pointed out in Chapter III, the functions of the root system are absorption, conduction, anchorage, and storage. We shall now discuss these four processes in the order named.

In considering the process of absorption we shall take up:

(*a*) Absorption of water.

(*b*) Absorption of inorganic salts.

Absorption of Water.—*Importance of Water in the Life of a Plant.*—Without water, the plant would be unable to carry on any of its life processes. Water is the largest component of all living tissue. The amount of water is usually greater in young, growing parts than in

FIG. 127.—Seedling of white clover (*Trifolium*) grown in moist air. The cotyledons have not yet escaped from the seed coat but the well-developed radicle shows clearly the growing point, region of elongation and root-hair zone. Magnification 6×.

FIG. 128.—Seedling of garden cress (*Lepidium*) grown in moist air. Root hairs in various stages of development can be distinguished behind the region of elongation. Surrounding the cotyledons is the swollen gelatinous mass derived from the seed coats. Magnification 4×.

older portions of the plant. In the case of seeds the non-living outer coats contain very little water. Water, however, is present in considerable quantities in the embryo and the living tissue which often accompanies it.

Water performs many functions in the plant, chief of which are the following:

1. It is a necessary component of protoplasm. Water constitutes about 80 to 90 per cent of the weight of active protoplasm. When, as in the case of dry seeds, the water content of the protoplasm is greatly reduced, there results a very great reduction in protoplasmic activity.

2. It is an essential raw material for food manufacture.

3. It serves as a solvent of gases (oxygen and carbon dioxide), and of mineral nutrients and foods.

4. It serves as a medium of transportation of raw materials and foods from place to place in the plant, since their transport can take place for the most part only in solution.

5. It makes possible the maintenance of turgor in living cells; the plant functions normally only when the cells are distended with water.

In arid and semi-arid regions scarcity of water is often the principal condition which limits the growth of plants. Our crop plants almost always have an abundance of light and oxygen and sufficient carbon-dioxide to permit normal growth; the temperature of the air and the soil practically never is seriously unfavorable to growth; moreover, the physical and chemical nature of the soil is for the most part suitable. In the principal agricultural sections of the country and particularly in semi-arid and arid regions, water is the principal limiting factor in crop production. That is to say, it is water shortage rather than any other unfavorable condition which prevents the plant from being more active than it is. Water is a most important factor determining both the distribution of plants over the earth's surface and the character of the individual plant. We observe marked dissimilarities in the vegetation of high mountains, dry plains, prairies, and the eastern deciduous forest belt; in the character of the plant life of tropical rain forests, the South American pampas, the Russian steppes, deserts, and tundras; and the vegetation of hillside, of brook bank, of gravel slope, of rock slide, of bog, of meadow and of the open water shows distinct variations. These variations are very largely due to differences in the supply of water.

In our crop plants, and most others, all water comes to the plant from the soil. As we have learned, the water enters the plant through the root hairs. We speak of this entry as **water absorption.** Water passes out of the plant principally through small openings (stomata) in the surface of the leaves. We speak of this water exit as

transpiration. There is a stream of water through the plant, from roots to leaves. Its rate of flow may be restricted at two points, the point of entry and the point of exit. Too much transpiration and too little absorption are the principal dangers to which the plant is exposed.

The Process of Absorption.—It is well to emphasize again the fact that all the functions performed by the plant are but the expression of the activities of individual cells. Absorption, together with other cell functions, was discussed in Chapter II. Here we shall discuss this process with particular reference to its performance by the roots.

All substances, either gases or solids, which enter the plant from the soil must be in solution in water, and must pass through the wall of the root hair and also through the cytoplasmic membrane which lines the wall. The cell wall, of cellulose, is a permeable membrane through which water and all solutes present in the soil solution can pass unhindered. The cytoplasmic membrane is, however, semipermeable. Normally, the total concentration of the solutes in the cell sap of the root hair is greater than in the soil solution outside the root hair. Under this condition, the movement of water is from the soil into the root hair, and this movement of water tends to go on just as long as the concentration within the root hair exceeds that outside. The rate of movement of water inward depends upon the relative concentration of the two solutions and this rate tends to decrease as the concentrations of the two solutions become more nearly equal. Water is, however, constantly being withdrawn from root-hair cells to the outermost cells of the cortex and thus the concentration of the cell sap of the root hairs remains fairly constant.

Water in the Soil.—If a dry soil is exposed to the air, and if the temperature is kept constant, it takes up water from the atmosphere until a condition of equilibrium between the moisture in the soil and that in the air is attained. This small amount of water, taken from the atmosphere, and held by the soil particles, is called **hygroscopic water.** It can be shown that most solid objects are covered by a film of hygroscopic water, which can not be wiped off and can only be removed by heating to a high temperature, and that the hygroscopic water of the soil is thus held upon the surface of the soil particles.

If water is added to a soil, which already contains hygroscopic moisture, by rain or irrigation, the water collects in the capillary spaces between the particles. The water is now held in the soil in the form of films and as wedge-shaped masses near the points of contact of the soil particles. The soil is now said to contain **capillary water,** or **film water.** Such water will not be drawn out of the soil by the pull of gravity.

If still more water is added to the soil, capillary water increases until, beyond a certain amount, the pull of gravity overcomes the capillary forces in the soil, and downward movement takes place. All the water which thus drains out of the soil when drainage is possible is known as **gravitational water.**

Whereas experiments have shown that certain plants may use some hygroscopic water, usually severe injury is evidenced long before this low moisture content is reached. On the other hand, if the pore spaces of the soil are filled with gravitational water, the supply of oxygen necessary for respiration of root cells is seriously restricted. Between these limits there appears to be a rather wide range of water content of the soil within which most agricultural plants seem to grow well.

Factors Affecting the Intake of Water from the Soil.—The principal factors influencing the absorption of water by the plant are the following:

1. Available water in the soil;
2. Rate of water movement in the soil;
3. Temperature of soil water;
4. Concentration of the soil solution;
5. Composition of the soil solution;
6. Extent of the root system;
7. Rate of transpiration.

(1) *Available Water in the Soil.*—As we have already stated, not all of the water in the soil is available for absorption. There is, in fact, no direct relation between the percentage of water in the soil and the amount available to the plant, because this amount varies with the nature of the soil. Wilting is the result of water loss exceeding water absorption. This relation may be the result of one of two conditions, namely: (1) absorption going on but at a slower rate than transpiration; (2) absorption no longer possible but transpiration continuing. In the former case, the stopping of transpiration or slowing it up very much is followed by recovery of the plant. In the latter case there is no recovery except by adding water to the soil, and in this case **permanent wilting** is said to have taken place.

Permanent wilting has been defined as that stage of wilting when the leaves first undergo a permanent reduction of their moisture content as a result of a deficiency in the soil moisture supply. By permanent reduction is meant a deficiency in the water content of the leaves from which they do not recover in an approximately saturated atmosphere, without addition of water to the soil.

The percentage of water (based upon dry weight) left in the soil when permanent wilting takes place is called the **wilting coefficient** of the soil.

As previously discussed, a cell must be in a state of turgor in order to enlarge. The enlargement phase of growth ceases when the cell is not completely turgid, that is, when it is in any stage of wilting. However, the water remaining in the soil after the wilting coefficient is reached may be drawn upon to keep the plant alive for a time, that is, to prevent fatal drying out or withering. Permanent wilting does not necessarily mean death of the plant, for if water is added to the soil, the plant will recover. It differs from a less severe stage of wilting, such as may occur during times of high transpiration, in that in the latter case, the cells may become turgid during a period of reduced transpiration, without any addition of water to the soil.

The residual water content of the soil when the plant begins to permanently wilt, that is, the wilting coefficient, varies with the soil. The water-holding capacity of a soil depends chiefly upon the size and arrangement of soil particles and upon the amount of colloidal material that is present. For example, a clay soil holds more water than a sandy soil. When a plant growing in a sandy soil has reached a point of permanent wilting, the amount of water left in the soil is less than that left in a clay soil under similar conditions. The wilting coefficient of a soil is expressed as a percentage of water based upon dry weight.

The accompanying table gives the wilting coefficient of different types of soil (data from Briggs and Shantz).

Type of Soil	Wilting Coefficient, Per cent
Coarse sand	0.9
Fine sand	2.6
Sandy loam	8.3
Loam	11.0
Clay loam	13.6

Here it is seen that after a plant has reduced the water in a sandy-loam soil to the wilting coefficient, 8.3 per cent of water is left in that soil. On the other hand, the same plant growing in a clay-loam leaves 13.6 per cent of water in the soil. Looking at this in another way, a sandy-loam soil having in it 13.6 per cent total water would be much " wetter " as far as the plant is concerned, than a clay-loam soil with the same amount of water. The plant growing in a sandy-loam soil with 13.6 per cent total water can reduce the water to 8.3 per cent; whereas, the same plant in a clay-loam soil with 13.6 per cent total water would permanently wilt.

It has usually been assumed that the greater drought resistance of one plant as compared with another was due to the differences in their ability to extract water from the soil. This would mean that the wilting

coefficient of a particular soil type varied according to the plants which grew in that soil. It has been experimentally determined, however, that under similar atmospheric conditions, the wilting coefficient of a given soil will be approximately the same no matter what plant grows on it. This is shown in the following table, which gives the relative wilting coefficients of a given soil when different varieties of plants are grown therein.

WILTING COEFFICIENT OF SAND LOAM
(Data from Briggs and Shantz)

Kind of Plant	Wilting Coefficient, Per cent
Corn (Boone County White)	6.5
Sorghum (Dwarf Milo)	5.9
Wheat (Kubanka)	6.3
Oats (Kherson)	5.9
Barley (Beldi)	6.3
Rye (Giant Winter)	5.9
Pea (Canada Field)	6.9
Vetch (*Vicia faba*)	6.1
Tomato (Stone)	6.9

It follows that the wilting coefficient varies widely in different types of soil but relatively little for different plants. It was stated by Briggs and Shantz that the wilting coefficient of a soil was independent of external environmental conditions. It appears, however, from certain subsequent experiments, that when there is a high transpiration rate, the wilting coefficient of a given soil is less than when the transpiration rate is low or moderate.

(2) *Rate of Water Movement in the Soil.*—If the rate of water absorption by the roots is high, and moisture is absorbed by the root hairs from the adjacent soil at a faster rate than soil conditions will allow it to be replaced from more remote soil layers, the soil immediately surrounding the root hairs will attain a water content which will result in wilting and consequently cessation of growth. This shows the importance of the rate of water movement in the soil. This complex property of a soil is dependent upon the water content of the soil per unit volume, the size and nature of the soil particles, and also their arrangement.

(3) *Temperature of Soil Water.*—The rate of absorption by the roots of plants is lowered by a decrease in soil temperature. A plant may even wilt in a soil saturated with water if the temperature of the soil sinks below a certain point. Winter killing is often the result of cold soil, accompanied by excessive transpiration, and thus is frequently caused by drying rather than by freezing.

(4) *Concentration of the Soil Solution.*—As has been mentioned, water passes from the soil through the cell wall and the cytoplasmic membrane of the root hairs into the root-hair cells. From these it passes to the adjacent cells and finally reaches all parts of the plant. This process of water intake and transport tends to go on **as long as the total concentration of the cell sap of the root-hair cells is greater than the total concentration of the soil solution surrounding the root hairs.** The greater the difference in the concentrations between the cell sap and the soil solution, the more rapid the water intake. If the concentration of the soil solution approaches that of the cell sap, the rate of absorption slows down. The roots of plants growing in an alkali soil are surrounded by a soil solution of high concentration, and absorption is retarded. In such cases there may be plenty of water present in the soil, but the plant can secure it only with great difficulty, on account of the high concentration of the soil solution. Although not "physically dry," such a soil is "physiologically dry." Plants growing in alkali soils usually show the same adaptations displayed by plants growing under desert and semi-arid conditions; those of alkali soils find it difficult to absorb water on account of the high concentration of the soil solution; those of the desert find it difficult to absorb water because the soil is actually deficient in water.

(5) *Composition of the Soil Solution.*—The influence of the composition of the soil solution upon the rate of intake of water by roots is well shown in the case of many bog plants. Such plants as cranberry and Labrador tea, for example, which are peculiar to bogs, have a poor development of roots and such plants have a low absorption in proportion to transpiration. This is held to be due to the toxicity of bog water. The toxins in bog water are believed to arise from the microorganisms of the water.

(6) *Extent of Root System.*—Based upon the distribution of the roots in the soil, two general types of root systems are recognized: (1) Those that penetrate deeply in the soil, and (2) those that are confined to surface layers. Some plants, alfalfa, for example, do not suffer from drought because of their ability to send their roots into the deeper and moister soil layers. If, on the other hand, the soil is shallow and rainfall light, plants with shallow root systems are likely to be relatively more successful than deep-rooted species, on account of their ability to take advantage of the water that comes to the soil in the form of occasional light showers. The depth of the root system of a plant is a character largely inherent in the plant, and is in a measure independent of external conditions.

The rate of extension of the roots, as well as the extent of the root

system, is a factor influencing the intake of water. As a root removes water from the soil immediately about it, there is a tendency for it to grow into moister soil zones. The rate of growth varies with the species of plant, and with the soil environment.

(7) *The Rate of Transpiration.*—The amount of water transpired by a plant during a given period is practically equal to that absorbed during the same period. The rate of entrance of water through the roots and its rate of movement in the plant are largely dependent upon the rate of transpiration. Such external conditions as light, relative humidity, temperature, and air movements, which directly influence the rate of transpiration, indirectly affect the rate of absorption.

Absorption of Inorganic Salts.—Land plants derive their inorganic salts from the soil. Among the inorganic salts which occur in the soil, the chief ones used by green plants are nitrates, phosphates and sulphates. Green plants derive nitrogen principally from nitrates; phosphorus from phosphates; and sulphur from sulphates; and the essential elements, potassium, calcium, magnesium and iron, are chiefly derived from salts which occur in combinations with either nitrogen, phosphorus or sulphur. These salts can enter the plant from the soil only when they are in solution.

It is important to keep in mind, however, that under similar conditions the **different mineral salts move into the plant independent of the passage of each other and of water.** As to the conditions governing the entrance of any particular solute into the plant, see the discussion on page 63.

We may picture the process of absorption by root hairs as one in which the molecules of water and the dissolved particles of many different salts are independently diffusing through cytoplasmic membranes of the root hair at varying rates, the rates depending in large part upon the quantity of each substance used by the plant.

Whereas substances pass from the soil through the cytoplasmic membrane into the root, it should be pointed out that, with the exception of water and carbon dioxide, substances in the root hairs are unable to pass into the soil. The supposition that under certain circumstances, sugar in the beet root, for example, passes from the root into the soil is not correct. The **percentage** of sugar in the root may fluctuate as a result of changes in the quantity of water present, but the **total quantity** of sugar in the root does not become appreciably less, except under very unusual circumstances, as when the stored supply is drawn upon to make an abundance of new leaf growth.

On the other hand, the excretion of carbon dioxide from the roots

has been satisfactorily demonstrated. It unites chemically with water to form carbonic acid, which aids in dissolving certain mineral compounds which are difficultly soluble in water.

FIG. 129.—The aerial or "prop" roots of corn (*Zea mays*) (After Robbins, from *Botany of Crop Plants.*)

Conduction by Roots.—Water which is absorbed by the root hairs passes by diffusion into adjoining cortex cells; by the same process it passes from one cortex cell to another, across the root to the tracheal tubes and tracheids of the xylem. It is carried upward in these elements to the stem. It will be recalled that in the young root, xylem and phloem elements occur in radiating groups, the groups of xylem elements alternating with the phloem groups. Hence, it is possible for the water to reach the xylem elements from the cortex without first passing across the phloem elements. There is some difference of opinion concerning the path of movement of dissolved mineral salts, which are absorbed by the root hairs. The most widespread belief is that they travel in the transpiration stream, but there is some evidence

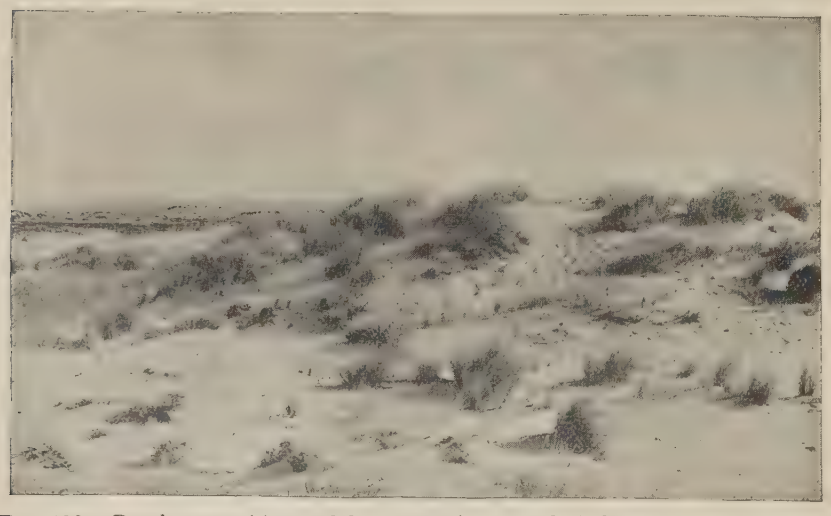


FIG. 130.—Beach grass (*Ammophila arenaria*), a sand-binding plant, growing on dunes near the seashore. (From photograph by Massart.)

indicating that these solutes are conducted in the phloem. It may be that both xylem and phloem are concerned in the upward movement of mineral salts.

There is considerable evidence that the mineral nutrients absorbed by the roots on one side of a large plant, like a tree, are mostly trans-

Fig. 131.—Indian banyan (*Ficus indica*). The horizontal branches of this tree may send out aerial roots which grow downward, become attached to the soil, and serve as "props" as well as absorbing organs.

located to and used by the trunk, limbs and leaves directly above them. There is apparently very little cross-transfer of such nutrients in the plant. However, it is believed that water may move through or around the plant without much difficulty.

Anchorage by Roots.—The roots of a plant are very effective anchorage organs. In most plants all roots perform the triple role of absorp-

tion, conduction, and anchorage. However, there are some plants (cacti, e.g.), that have two sorts of roots, those which are mainly for anchorage and those which are chiefly concerned with absorption. The hold which roots have on the soil is well shown in plants of sand dunes, where the soil is constantly shifting; mounds of sand are held in place by the mat of roots (Fig. 130).

Storage by Roots.—The roots of many plants store food and water. Such roots may become large and fleshy, familiar examples being the sugar beet, turnip, dahlia, radish, carrot, parsnip, and sweet potato. Many plants with fleshy roots are cultivated for their roots alone and are called "root crops." Sugar and starch are the principal forms of food stored in such roots. The sugar beet, for example, contains approximately 15 per cent of cane sugar. The sweet potato, turnip, radish, carrot, and parsnip have considerable quantities of stored starch. Among our native plants, the most striking examples of fleshy-rooted plants occur in arid regions. A notable example is *Ipomaea pandurata*, popularly known as "man-of-the-earth," which may have storage roots weighing fully as much as a man. Storage roots are an advantage to plants that are subjected to periods of extreme drought.

FIG. 132.—Clustered fleshy roots of dahlia. (From Bocquillon.)

Reproduction by Means of Roots.—Some plants send up stems (so-called "suckers") from adventitious buds which arise on roots. This habit is well illustrated by the silver leaf poplar (*Populus alba*), and black locust (*Robinia pseudacacia*). Plants which do not normally produce adventitious root buds may be induced to do so by injury. For example, if the shoot of such plants as red raspberry, some roses, and common barberry (*Berberis vulgaris*), is cut down at the ground line, the roots send forth new stems. This ability of the roots of some plants to produce adventitious buds is made use of in the propagation of certain economic plants. Roses, raspberries, some blackberries, and a number of other plants are frequently propagated by root cuttings.

CHAPTER VI

THE LEAF

From the point of view of morphology, the leaf may be defined as an expanded, lateral outgrowth of the stem, arising at a node, and having a bud in its axil. The principal physiological characteristic of the leaf is its special adaptation to perform the functions of photosynthesis and transpiration. In most cases the leaf combines both the morphological and the physiological characteristics which have been mentioned. There are, however, structures such as bud scales, spines, and food-storing bulb scales, which do not perform the functions of typical leaves but which are nevertheless morphologically leaves. They are not well fitted to carry on photosynthesis and transpiration and are clearly adapted to some other special function. Because they arise at nodes or have buds in their axils, or for other reasons, these structures can be recognized, however, as foliar (leafy) in nature.

THE ORIGIN AND DEVELOPMENT OF THE LEAF

The leaf has its origin as an outgrowth or protuberance from the primordial meristem of the growing point of the stem within the bud (see Figs. 54 and 55). Such an outgrowth is called a **leaf primordium.** At first its growth is mostly apical (i.e., at the tip), but before it has reached any considerable length all of its cells begin to undergo active division and growth. From then on, growth goes on throughout the leaf. Growth of this sort, which is not restricted to the apex of the structure concerned, is called **intercalary growth.** The rudimentary leaves within the bud soon grow in length sufficiently to reach beyond the end of the growing point of the stem which, it will be recalled, lacks a special protective cap such as is produced by the root. Overlapping one another, they form an envelope which protects the growing point of the stem from desiccation, mechanical injury, and the ill effects of too much water. In the case of plants such as the apple (*Malus*), oak (*Quercus*), and maple (*Acer*), which form winter buds, the lowest leaf primordia develop into bud scales.

By reason of their tough texture, dark color, and more or less waterproof nature, bud scales are specially adapted to protect the parts within the bud. They do not develop into typical foliage leaves but are shed at the beginning of the growing season. The assumption that bud scales are really modified leaves is strengthened by the frequent occurrence of structures intermediate between bud scales and foliage leaves. A series of such structures from typical scales to typical leaves is shown in Fig. 133. In such buds the rudimentary leaves which are to develop into foliage leaves cease growing shortly after they are formed and they do not develop further until the following spring. Then the leaves of each developing bud "come out" of the bud in succession from the lowermost toward the growing point. This results from the elongation

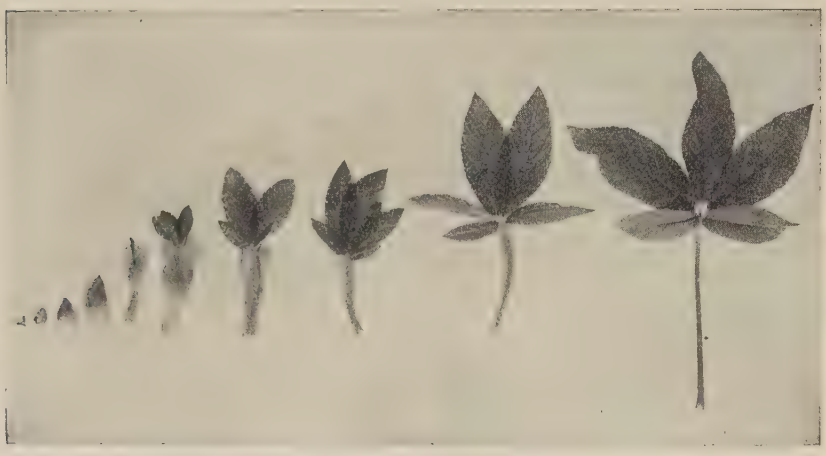


FIG. 133.—A series of bud scales and leaves of buckeye (*Aesculus*) showing intermediate stages indicating that bud scales are actually reduced foliage leaves.

of the internodes within the bud in succession from the base of the bud upward. As each internode lengthens, the leaf or leaves at its base come out of the bud and the bud is raised above this leaf. As soon as they are thus freed from the bud these leaves resume development and quickly grow to their full size. At this time it is easy to demonstrate that their growth is intercalary. All that is necessary is to mark off the surface of a young leaf, which is just emerging from the bud, into squares by means of Chinese ink or some other material which will not injure the leaf (Fig. 134). When such a leaf has attained its full differentiation, there are, as in the stem and root, epidermal cells, parenchyma cells, phloem and xylem elements, collenchyma, bast fibers, and other specialized cells. There is, however, no cambium in leaves

and therefore there is no secondary growth of vascular bundles or development of cork except that which is formed at the base of the leaf when it is shed.

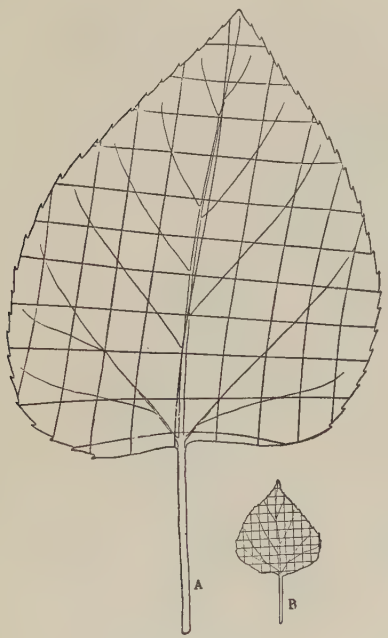


Fig. 134.

Fig. 135.

Fig. 134.—A poplar leaf (*B*) just after its release from the bud and (*A*) after it has grown to maturity. When the leaf was in the condition shown in *B* it was marked into squares with Chinese ink. Note that all the squares have increased in size as the leaf grew but that their form has undergone little change, which indicates that growth has gone on at about the same rate in all parts of the leaf.

Fig. 135.—A portion of a stem of pimpernel (*Anagallis*), showing the sessile leaves.

EXTERNAL MORPHOLOGY OF THE FOLIAGE LEAF

A typical leaf consists of three parts: (1) the expanded **leaf blade** or **lamina,** (2) the slender stalk or **petiole,** and (3) the broadened attachment to the stem which is called the **leaf base.** Frequently there are outgrowths, sometimes leaf-like, known as **stipules,** from either side of the leaf base. They are lacking in many plants; whereas in others they become detached and fall off soon after the leaves come out of the bud. Some leaves have no petioles and are said to be **sessile** (Fig. 135).

The Leaf Blade.—The form of the leaf blade is such as to provide a large surface for the absorption of the light energy needed in photosynthesis and for water loss through transpiration. On account of the thinness of the leaf blade, none of the cells lie far from the surface.

FIG. 136.—A branch of European linden, its leaves forming a mosaic.

This is of advantage in that the absorption of carbon dioxide by the green cells for sugar manufacture is facilitated, but a disadvantage in that a greater water loss through transpiration is made possible. This thin sheet of leaf tissue is strengthened by the midrib and veins, which also serve to conduct raw materials throughout the leaf and to carry away the food which the green cells manufacture.

The Petiole.—The petiole attaches the blade, which is the essential part of the leaf, to the stem, and conducts materials to and from the leaf blade. It is responsible for maintaining the blade in the position most favorable for the performance of its functions. The petioles of many plants are able to increase in length and to curve, so that the leaf blades are brought into the most favorable position regardless of whether the stem to which they are attached is perpendicular, oblique, or horizontal. The resulting arrangement is often such as to practically eliminate any shading of one leaf by another of the same plant. In such cases the leaves are frequently so fitted into the spaces between one another as to almost entirely utilize the available space. They are then said to form a **leaf mosaic** (Fig. 136).

FIG. 137.—Compound leaf of garden pea (*Pisum sativum*). Note the large, leaf-like stipules, and upper leaflets, modified as tendrils. (From Bocquillon.)

The Leaf Base.—The broadened form of the leaf base provides a firm attachment to the stem, which, in some plants, is partly or completely encircled by the leaf base. In the monocotyledons the leaf base usually forms a long sheath which surrounds the stem. In the grasses (*Gramineae*), in certain of the Musaceae, to which the banana belongs, and in some other monocotyledons, these sheaths protect the stem at the base of the internodes where its tissue long remains soft and capable of growth. In young grasses and in the banana, these sheathing leaf bases are principally responsible for the mechanical strength of the shoot.

Stipules.—When these structures are present they may serve various functions. In some plants, such as fig (*Ficus*) and the tulip tree (*Liriodendron*), they protect the parts within the bud. Often they are large and closely resemble the leaf blades. They then share the functions of the blade. For example, in *Lathyrus aphaca* the stipules have taken over entirely the typical functions of the blade, which is reduced to a tendril. They form spines in the black locust (*Robinia*), and in certain species of spurge (*Euphorbia*), and tendrils in some species of smilax.

Venation.—There are two principal types of arrangement of veins: **parallel veining** and **net veining** (Fig. 138). In parallel-veined leaves, the veins that are clearly visible to the unaided eye run parallel to each other. This kind of venation is characteristic of the monocotyledons. The parallel veins may run lengthwise of the leaf, as in the grasses, converging somewhat at the base of the blade and at the tip; or they may be directed outward from the midrib to the margin of the leaf, as in the banana (*Musa*). When a parallel-veined leaf is examined with a lens it can be seen that small veinlets connect the parallel veins.

If the veins that are visible to the naked eye branch frequently and join again, so that they form a network, the leaf is said to be net-veined. The leaves of dicotyledons have this type of venation but it rarely occurs among monocotyledons.

Net-veined leaves that have a single primary vein or midrib from which the smaller veins branch off, somewhat like the divisions of a feather, are **pinnately veined.** Common examples of pinnately veined leaves are the willow (*Salix*), the beech (*Fagus*), the apple (*Malus*), the oak (*Quercus*), the lilac (*Syringa*), and many other common plants. When there are several principal veins spreading out from the upper end of the petiole the leaf is said to be **palmately veined.** Among the many plants having palmately veined leaves are the maple (*Acer*), the geranium (*Pelargonium*), grape (*Vitis*), and pumpkin (*Cucurbita*).

Form of the Leaf Blade.—Leaves are said to be **simple** when, as in most plants, the blade is all in one piece (Fig. 139). Simple leaves frequently have the blade made up of a number of lobes separated by deep clefts or **sinuses.** Familiar examples of such simple **lobed leaves** are those of the oak (*Quercus*), maple (*Acer*), and sycamore (*Platanus*). The sinuses of pinnately veined, lobed leaves are always directed toward the midrib. In such cases the leaves are said to be **pinnately lobed** (Fig.140). Lobed leaves which are palmately veined are always **palmately lobed** (Fig. 140), the sinuses being directed toward the base of the blade where it is attached to the petiole. Oak leaves are pinnately lobed and maple leaves palmately lobed.

In many plants, such as most ferns, the potato (*Solanum tuberosum*),

beans (*Phaseolus*), peas (*Pisum*), clover (*Trifolium*), and the horse chestnut or buckeye (*Aesculus*), the leaf blade is made up of a number of separate leaf-like parts, or **leaflets.** Such a leaf is said to be compound

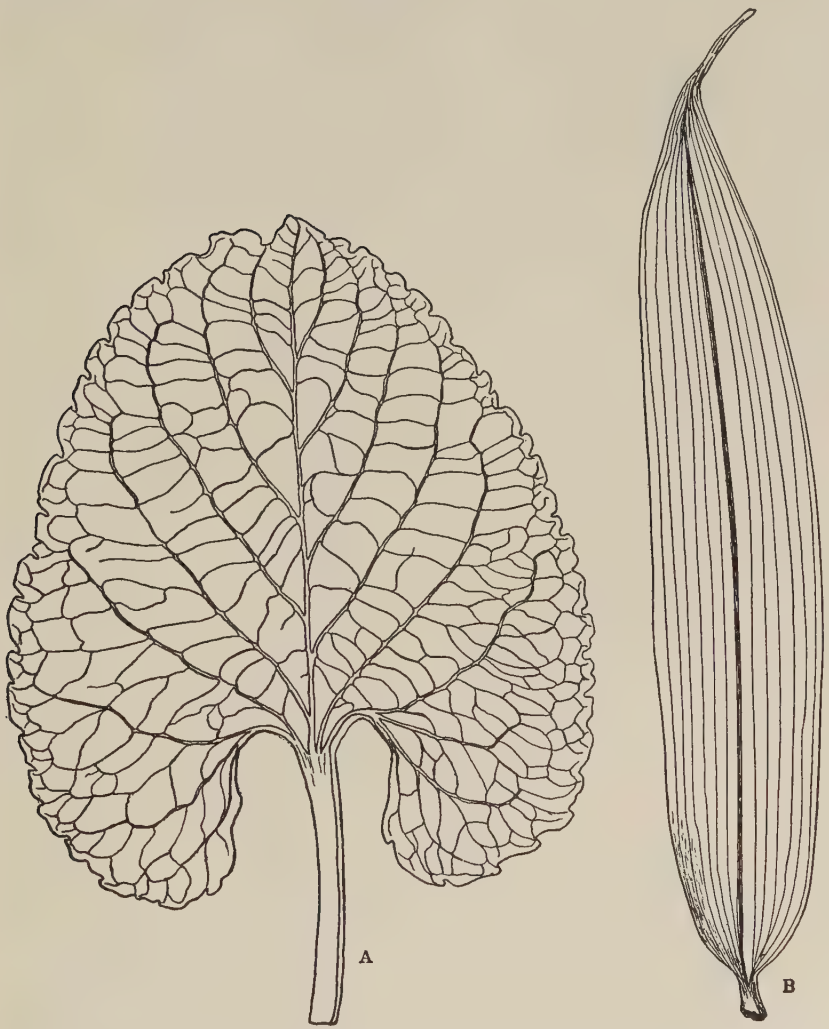


Fig. 138.—The two principal types of veining. *A*, Net veining as illustrated by the leaf of violet (*Viola*); *B*, parallel veining illustrated by the leaf of one of the bamboos. (*Arundinaria.*)

(Fig. 140). When, as in the case of the horse chestnut and clover, the leaflets are attached directly to the end of the petiole the leaves are said to be **palmately compound** (Fig. 140). If the petiole is extended into

FIG. 139.—Simple leaf of pear, showing stipules.

FIG. 140.—*A*, The simple, pinnately veined leaf of a plum (*Prunus*); *B*, the pinnately lobed, and pinnately veined leaf of an oak (*Quercus*); *C*, the palmately lobed and palmately veined leaf of a maple (*Acer*); *D*, the palmately compound leaf of wood-sorrel (*Oxalis*); *E*, the pinnately compound leaf of walnut (*Juglans*).

a long slender structure, corresponding to the midrib of an entire leaf, and if the leaflets arise at intervals along this structure, the leaf is **pinnately compound** (Fig. 140). In the case of such leaves the slender part to which the leaflets are attached is called the **rachis.** The leaves of the pea, the blackberry (*Rubus*), most ferns, and the potato are of this type. It is not always easy to distinguish a pinnately compound leaf from a leafy stem. The lack of a terminal bud, and the absence of lateral buds from the axils of the leaflets are sufficient to prove that a structure whose nature is in question is a compound leaf and not a leafy stem. Compound leaves are rarely met with in the monocotyledons.

The edge (**margin**) of the leaf may be smooth, as in most grasses, in onion (*Allium*) and in many other plants, or it may be variously toothed, as in the oak, rose, apple, cherry, etc. In the latter case the teeth may vary greatly in size and form. The systematic botanist uses many different terms to distinguish these differences in the nature of the leaf margin.

In most grasses there is an outgrowth, called the **ligule,** arising from the upper and inner side of the leaf blade where it joins the sheath (Fig. 141). In some grasses, such as barley (*Hordeum*) and timothy (*Phleum pratense*), this structure is scale-like; in others, for example, Bermuda grass (*Cynodon dactylon*), it consists of a row of stiff hairs or bristles. It is believed that the ligule serves to prevent the water which drains downward from the leaf blade from collecting inside the leaf sheath. In some grasses such as barley (*Hordeum*), there are also two little projections called **auricles** which grow out from the opposite sides of the sheath at its upper end (Fig. 141).

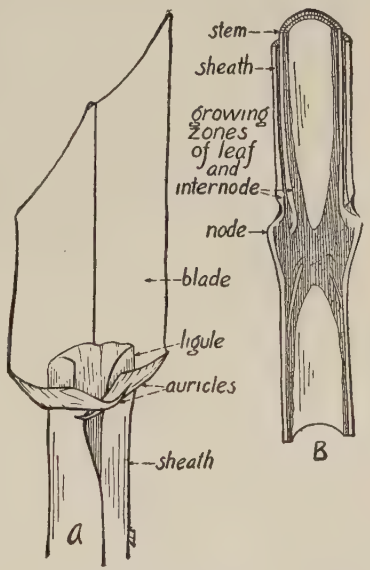


FIG. 141.—*A*, Portion of leaf of barley at juncture of sheath and blade; *B*, stem cut in median lengthwise section. ×2½. (After Robbins, from *Botany of Crop Plants.*)

ANATOMY OF THE LEAF

Microscopic examination of a typical foliage leaf shows that there are three kinds of tissue present: (1) the epidermis, (2) the mesophyll, and

(3) the vascular bundles (Figs. 142 and 143). The **epidermis** covers the whole leaf surface and protects the tissues within; the **mesophyll** is made up of parenchyma cells, most of which are green and able to carry on photosynthesis. The **vascular bundles,** or **veins,** consist of conducting elements for the transfer of water and inorganic salts and of foods.

The Epidermis.—The total area of the leaves makes up a very large part of the plant surface which is exposed to the air. On this account, the ability of the epidermis of the leaf to retard transpiration is of the utmost importance to the plant. Plants living in a habitat where the water available for absorption by the roots is limited, and where the dryness of the atmosphere favors rapid transpiration, are prevented

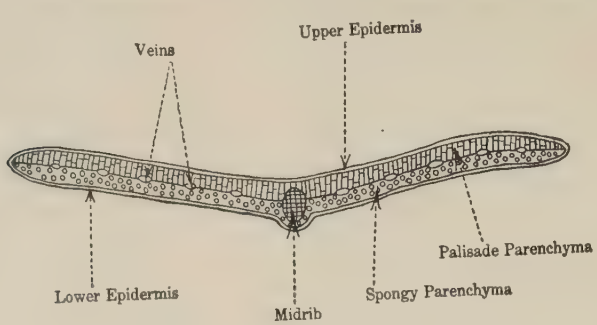


FIG. 142.—Diagram of a cross section of a typical foliage leaf.

from dying of water shortage only by the ability of the epidermis to keep the rate of water loss below that of water absorption.

The leaf epidermis of many plants may be stripped off with little difficulty. It is generally easier to remove it from the under side than from the upper side of the leaf. This is due to the fact that the mesophyll of the lower half of the leaf is a very loose tissue with many intercellular spaces and therefore with fewer points of attachment to the epidermis than the compact mesophyll which lies below the upper epidermis.

When a piece of epidermis from the lower side of a leaf is examined under the microscope it is found to be made up of two kinds of cells, **ordinary epidermal cells** and **guard cells.** As seen in surface view, the ordinary epidermal cells generally have a wavy outline (Fig. 144). They are about as broad as they are long in most plants, but in the grasses and many other monocotyledons having long, narrow leaves, they are elongated in the direction of the long axis of the leaf. In leaf cross sections it can be seen that the depth of the ordinary epidermal

cells is considerably less than their breadth or length (Fig. 146). Chloroplasts are usually absent from these cells. The outer wall of ordinary epidermal cells generally averages between .003 and .004 millimeter in thickness, but it gives very effective protection against mechanical injury not only by reason of its toughness but also because of the sup-

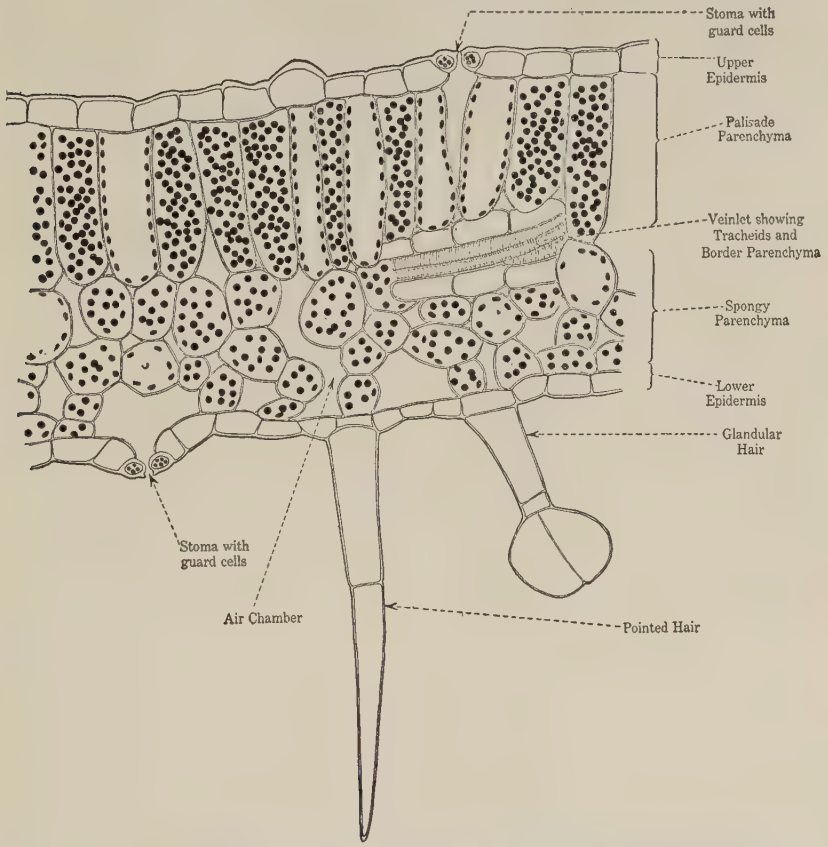


FIG. 143.—A cross section of a portion of a leaf of potato (*Solanum tuberosum*). Except for the chloroplasts none of the cell contents have been shown. Some of the cells of the palisade and spongy parenchyma have been shown in section, others in surface view.

port given it by the radial walls. It has been computed that beneath a square millimeter of the outer epidermal wall of the leaves of many common plants there are more than 2000 radial walls. These oppose the penetration of the epidermis by any object not having an exceedingly sharp point. The cuticle of the leaf epidermis, like that of the epidermis

of the stem, is made up almost entirely of the waxy, waterproofing substance, **cutin.** The wall layer below the cuticle is, in many plants, made up of both cellulose and cutin and is then spoken of as the **cutinized layer.** The innermost part of the outer wall and all of the other walls of the epidermal cells are almost pure cellulose.

In addition to its protective function, in certain xerophytic plants the leaf epidermal cells are very large and are thought to serve as a water-storing tissue from which the mesophyll cells can draw temporarily during periods of water shortage.

The protoplasts of the epidermal cells are long-lived; they do not die until just before the leaf falls. The cytoplasm forms a very thin

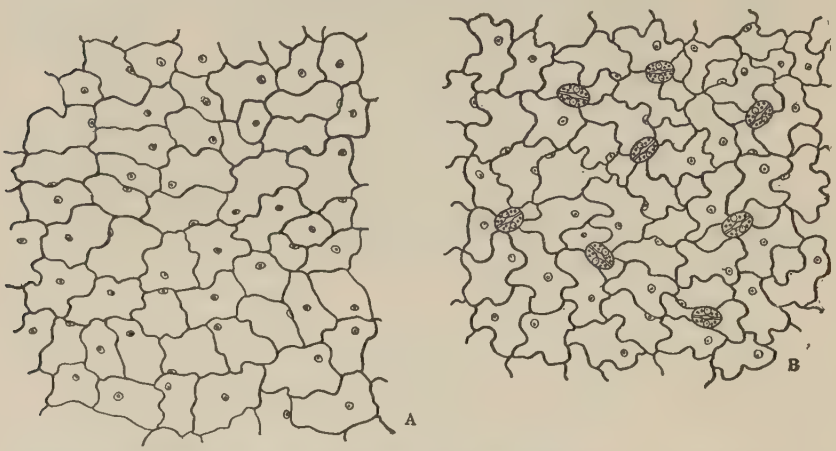


FIG. 144.—Surface view of the epidermis of a typical foliage leaf. *A*, From the upper surface of the leaf; *B*, from the lower surface. The cytoplasm of the cells has not been shown.

layer surrounding a large vacuole and the nucleus and nucleolus are often very conspicuous.

Guard Cells and Stomata.—Scattered among the ordinary epidermal cells of the lower epidermis, and sometimes of the upper epidermis also, are the guard cells. These occur in pairs, and when seen in surface view appear broadly crescent-shaped or almost semicircular in form (Fig. 145). The more or less concave sides of the guard cells are turned toward each other, and between them there is an opening or pore which leads from the outside into a large air chamber in the mesophyll. This opening between the guard cells is the **stoma** (plural, **stomata**). The cuticle of the leaf is generally very impermeable to oxygen and carbon dioxide and to water vapor. The passage of these three gases into or out of the leaf takes place very largely through stomata.

By means of a very simple experiment it is possible to show how very impermeable to water vapor the cuticle may be and with what readiness

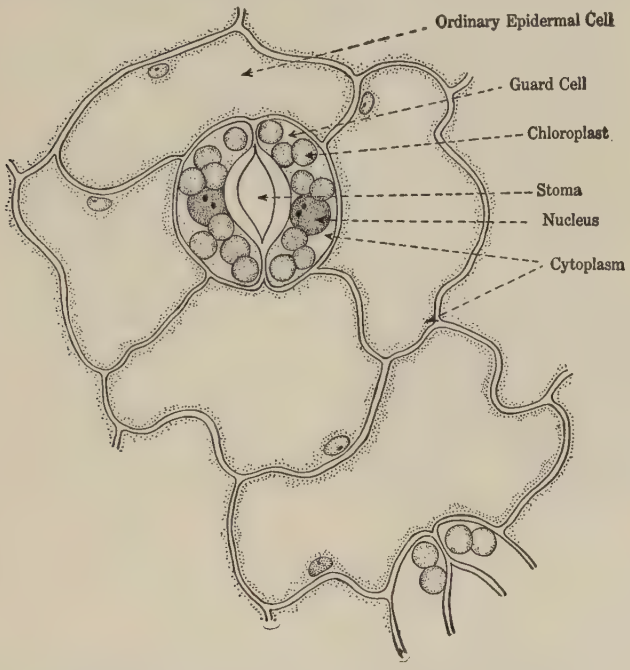


FIG. 145.—A view showing in detail a small portion of the epidermis from the upper surface of a typical leaf.

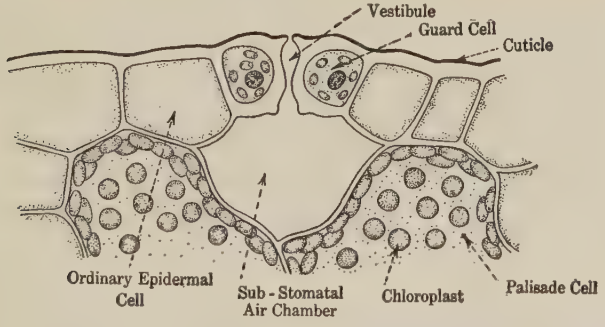


FIG. 146.—A portion of a cross section of a foliage leaf showing a stoma and a few of the neighboring cells. (Redrawn after Kny.)

water is lost through the stomata. The tropical *Ficus elastica*, or rubber plant, which is a common house plant, has leaves which serve well for this experiment, for the cuticle is thick and the stomata are all found on

the under side of the leaves. The leaves of several species of magnolia will serve equally well. If two similar leaves of this plant are removed and one is smeared with vaseline on the upper surface and the other on the lower surface, the former will begin to shrivel and dry up after a few days' exposure to the dry air of the laboratory, while the leaf whose lower surface has been smeared with vaseline will remain almost normal in appearance for weeks. This difference is due to the fact that the smearing of the under surface seals up the stomata so that little water is lost from the under side of the leaf, while covering the upper leaf surface with vaseline is almost without effect upon the already very low rate of water loss through the cuticle, and leaves the water in the leaf tissues free to pass out through the stomata of the under side.

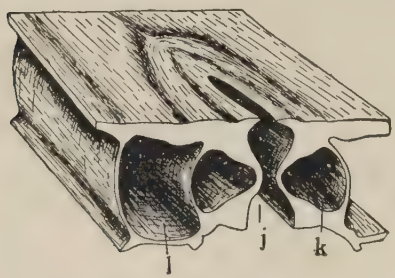


FIG. 147.—Diagram showing a typical stoma and adjoining epidermal cells as seen in surface view and in cross section. *J*, stoma; *k*, guard cell; *l*, epidermal cell bordering a guard cell. (After Stevens.)

The guard cells have numerous, conspicuous chloroplasts. In cross sections of the leaves of many kinds of plants it can be seen that the guard cell walls adjacent to the stoma are of greater average thickness than elsewhere. There may also be observed ridge-like outgrowths from the walls of the guard cells, which form a chamber, outside the stoma proper (Fig. 148). Sometimes this "vestibule" has only a narrow, slit-like opening to the outside. In xerophytic plants the ordinary epidermal cells may overlap the guard cells so that the stoma and guard cells are depressed below the general surface of the epidermis. Plants growing in very moist habitats may, on the other hand, have the stomata raised above the surrounding epidermal cells (Fig. 150).

Control of Stomata by the Guard Cells.—The guard cells are able to open and close the stomata. Thus they regulate the entrance and exit of gases. The opening and closing of the stomata by the guard cells depend upon changes in the turgor of these cells. When the turgor of the guard cells becomes greater than that of the adjacent cells, the stomata are opened; when it is equal to that of the neighboring cells or when excessive water loss greatly reduces the turgor of all the living cells of the leaf, the stomata are closed. Illumination of the guard cells increases the concentration of sugar in their cell sap. This is generally assumed to be due to photosynthesis by the illuminated chloroplasts. However, in some cases at least, it seems to be caused also by a change

in the acidity of the sap of these cells which in turn favors the digestion

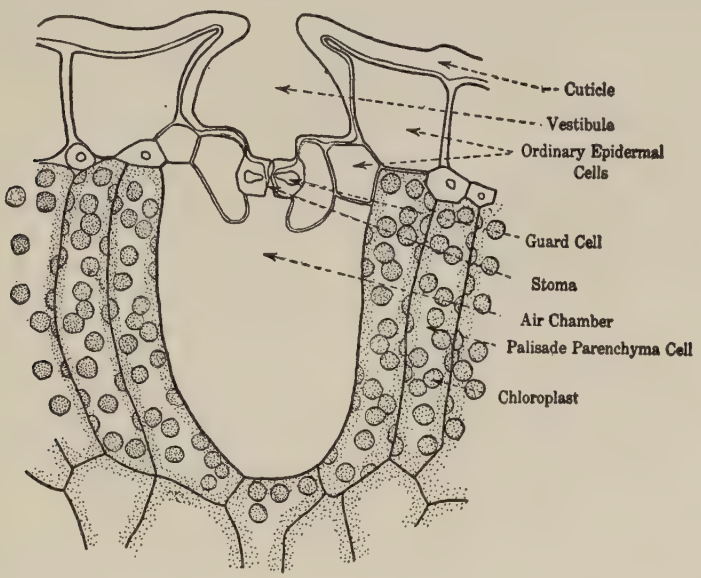


FIG. 148.—Depressed stoma of *Hakea suaveolens*. (In part after Haberlandt.)

of the starch in the guard cells to sugar. In either case the sugar content of the sap of these cells increases. This sugar raises the concentration of the cell sap above that of the cell sap of the surrounding ordinary epidermal cells which are without chloroplasts or contain only a few small ones. As a result, the guard cells withdraw water from the ordinary epidermal cells and their turgor increases while the turgor of the surrounding cells decreases.

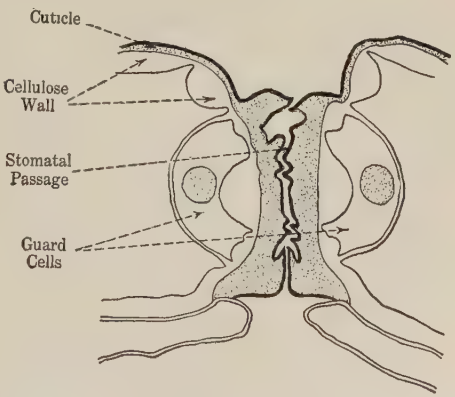


FIG. 149.—A cross section through a stoma from the under leaf surface of *Nipa fruticans*. Note the tortuous passageway between the guard cells. (From Bobisut.)

In one of the commonest and simplest cases, the walls farthest from the stoma, having less average thickness than those next to it, stretch and bulge outward, drawing with them the walls adjacent to the

stoma. The displacement of the walls bordering on the stoma is much less than that of the thin walls farthest from it but is still sufficient to leave a clear passage between the guard cells. At night or when the leaf is strongly shaded, the concentration of sugar in the guard cells becomes less because the accumulated sugar soon diffuses out of the guard cells or is changed to starch. As a result the differences in cell sap concentration which cause the opening of the stoma no longer exist. The stretched walls of the guard cells shorten, and the stoma is

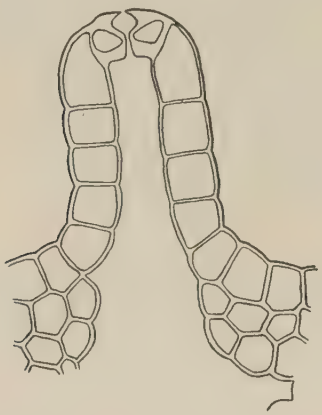


Fig. 150.

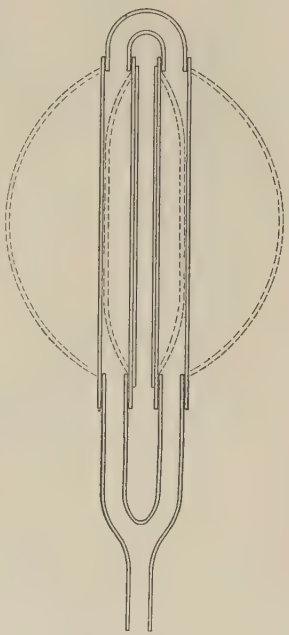


Fig. 151.

Fig. 150.—Raised stoma from the fruit stalk of pumpkin (*Curcurbita pepo*). (After Haberlandt.)

Fig. 151.—Diagram of a model illustrating the manner in which the stoma is opened when the turgor of the guard cells increases. The short, glass U-tube at the base is connected to the Y-tube, also of glass, by two pieces of rubber tubing. The inner (adjacent) walls of these two pieces of tubing are made thicker than their outer walls. The thicker portions of the walls of the rubber tubing correspond to the guard cell walls next the stoma, whereas the thinner portions of the walls of the rubber tubing correspond to the guard cell walls furthest from the stoma. If water or air are forced under pressure into the Y-tube and the rubber tubing thus subjected to internal pressure, the greater extensibility of the thin, outer walls causes them to take the position shown by the outer dotted lines in the diagram. As the result of this bulging of the outer walls of the rubber tubes the inner, thick walls are drawn apart as shown. Thus, under pressure from within the tubes, the space between the tubes is widened, corresponding to the opening of the stoma. When the pressure is reduced the inner walls tend to return to their original position, narrowing the opening between them, as when the stoma is closed by the guard cells.

closed. If a leaf with open stomata is placed in a solution of higher concentration than the cell sap of the guard cells, or if it is taken suddenly from a very moist atmosphere to a very dry one, the stomata, as a result of water being withdrawn from the guard cells, may close even though the leaf is brightly illuminated. The accompanying figure (Fig. 151) shows a model of a stoma and guard cells of the simple type previously described.

We may summarize the above discussion as follows: the stomata **open when the turgor of the guard cells rises**; increased turgor of the guard cells is due to an increase in the concentration of their cell sap which enables them to absorb water from neighboring cells; increased concentration of the cell sap is due to an accumulation of sugar in the guard cells; sugar accumulates when the guard cells are illuminated or when a change in the acidity of the guard cell sap favors the digestion of starch to sugar. The stomata **close when the turgor of the guard cells falls**; decreased turgor of guard cells is due to a decrease in the concentration of their sap which lowers their power to absorb water from adjacent cells; decreased concentration of the sap of guard cells chiefly results from the movement of sugar from them or its change to starch and the storage of the latter temporarily in the guard cells.

Epidermal Hairs.—Many leaves have hairs which grow out from the epidermis. The simplest of these hairs are mere extensions of epidermal cells, the hair and the epidermal cell being in such cases a single cell. Such unicellular hairs are common on the leaves of plants belonging to the Cruciferae or Mustard Family. Multicellular epidermal hairs, consisting of a single filament of cells which decrease in diameter from the base to the apex, are much more common than are unicellular hairs. This type of hair is found on the squash and most other members of the Cucurbitaceae, on the geranium (*Pelargonium*), and on many other common plants. Both unicellular and multicellular hairs may be branched, as in mullein (*Verbascum*), and various members of the Malvaceae or Mallow Family. The branched epidermal hairs of many mallows are stellate, consisting of a short stalk from the upper end of which a number of branches radiate out at right angles like the points of a star. Some plants such as the chinquapin (*Castanea chrysophylla*), the buffalo berry (*Shepherdia*), and oleaster (*Eleagnus*) bear shield-shaped hairs which consist of a scale-like expansion at the end of a short stalk. Glandular hairs bear at the upper end a rounded head which may consist of a single large cell or of a group of cells, and which often secretes an ethereal oil. The secretion from these glandular hairs is frequently very viscid and sticky as in the case of the tarweeds (*Madia*

and *Hemizonia*) and tobacco (*Nicotiana*). Other familiar examples of plants bearing glandular hairs are the Chinese primrose (*Primula sinensis*), and the pumpkin, squash, and various other Cucurbitaceae.

The Mesophyll.—The upper and lower surfaces of typical foliage leaves are usually distinctly different in appearance. The upper surface is generally darker than the lower, and the larger veins which project out from the surface on the under side are, on the upper side,

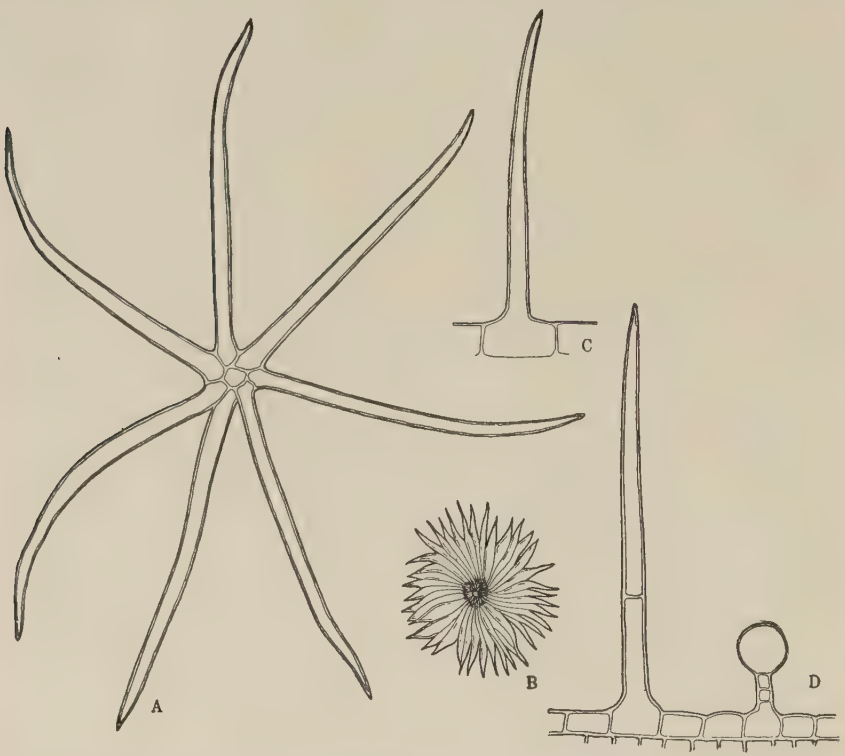


FIG. 152.—Several types of epidermal hairs. *A*, branched hair of false mallow (*Malvastrum*), this hair is attached to the leaf by a short stalk not shown in the drawing. *B*, scale-like stellate hair of *Eleagnus*, its centrally attached stalk not shown. *C*, pointed, unicellular hair of shepherd's purse (*Capsella*). *D*, a pointed multicellular and a capitate, glandular hair of geranium (*Pelargonium*).

even with the leaf surface or depressed below it. When epidermal hairs are present they are generally much more abundant on the lower than on the upper side and they are frequently restricted to the lower side of the leaf. Leaves with such differences between the two sides are called **dorsiventral leaves** or **bifacial leaves** (Fig. 153). These differ-

ences between the two surfaces of a dorsiventral leaf result from the fact that such a leaf is held in a horizontal or oblique position by the petiole. In the case of the adult type of leaf in *Eucalyptus* and of most other

Fig. 153.—Leaf dimorphism in *Eucalyptus*. The branch to the left shows the sessile, dorsiventral, juvenile type of leaf, found on seedlings, very young plants, and suckers. The branch to the right shows the stalked, pendent, isobilateral adult type found on older plants except where they have been cut back.

plants whose leaves hang perpendicularly downward, or are held erect, and are therefore equally illuminated on both sides, the two surfaces are similar. Such leaves are called **isobilateral leaves.**

The mesophyll of typical dorsiventral leaves is made up of three kinds of tissue: the **palisade parenchyma,** the **spongy parenchyma,** and the **border parenchyma** (Fig. 154). The palisade parenchyma consists of from one to several layers of elongated cells placed with their long axes at right angles to the leaf surface. This tissue extends downward from

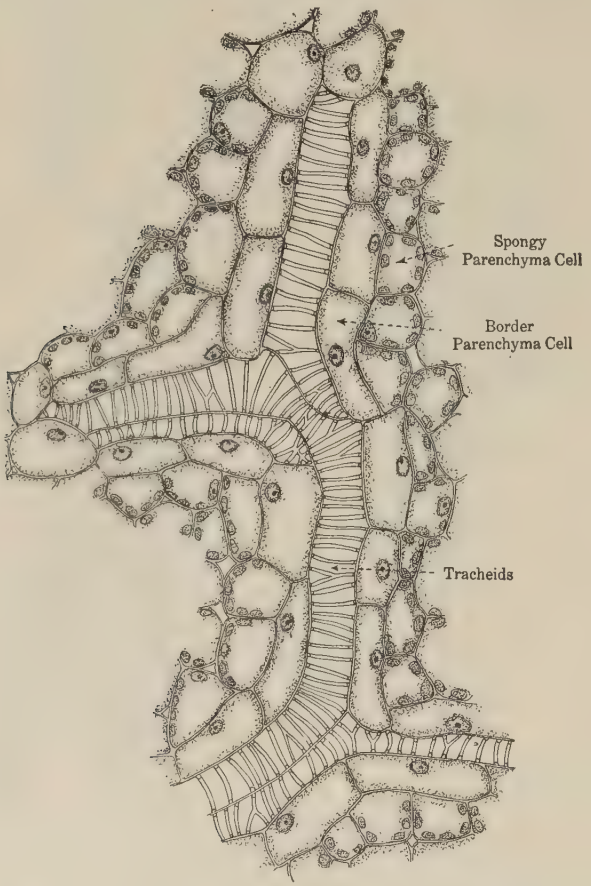


FIG. 154.—A section cut parallel to the leaf surface and through the spongy parenchyma. The free ends of several veinlets are shown as well as the relation of border parenchyma and spongy parenchyma cells to the finest veins.

the upper epidermis to the spongy parenchyma. The latter tissue forms the lower portion, generally somewhat more than half, of the mesophyll. The spongy parenchyma cells are not elongated like the palisade cells. Their form and arrangement are such that numerous large intercellular spaces exist between them. Border parenchyma forms a single-layered

sheath surrounding the conducting elements of the veins. The cells of the palisade and spongy parenchyma contain chloroplasts. Those of the border parenchyma are without chloroplasts.

The Palisade Parenchyma.—Although this tissue is much more compact than the spongy parenchyma, intercellular spaces are by no means absent. These spaces are smaller than those of the spongy parenchyma but they are so distributed that every palisade cell is in contact with an intercellular space, and each such space communicates with the system of connecting intercellular spaces in the spongy parenchyma. Thus there is provision for the free access of carbon dioxide and oxygen to all the food-making cells of the mesophyll. On account of their position the palisade cells receive more illumination than the spongy parenchyma cells. They are more abundantly provided with chloroplasts than are the latter cells. According to estimates made by the plant anatomist, Haberlandt, the palisade cells of 1 square millimeter of the leaf of the castor oil plant (*Ricinus communis*) contain over 403,000 chloroplasts; while there are only 92,000 in the spongy parenchyma cells of the same area. The deeper green of the upper surface of most dorsiventral leaves is due to the greater number of chloroplasts and the smaller number and size of the intercellular spaces of the palisade tissue as compared with those of the spongy parenchyma. In isobilateral leaves palisade parenchyma is generally found on both sides. In such cases there is frequently a layer of spongy parenchyma between the two layers of palisade tissue.

The Spongy Parenchyma.—As has been stated, in most leaves the number of stomata in a given area is greater on the lower than on the upper side, and in the case of many plants there are no stomata whatever on the upper side. In such leaves the supply of carbon dioxide to the palisade cells during periods of active photosynthesis would be insufficient were it not for the loose nature of the spongy parenchyma. The light which reaches the spongy parenchyma cells is much less intense than that which falls upon the palisade tissue, for the former are shaded by the palisade parenchyma above them and the light which reaches them from below is, of course, much weaker than that which falls upon the upper surface of the leaf.

The Border Parenchyma.—Although the vascular bundles of the petiole and of the large veins contain tracheal tubes, tracheids, sieve tubes, and companion cells, the finest branches of the veins are made up entirely of tracheids. At the extreme end of one of these branches the vascular bundle is reduced in many cases to a single tracheid. Most of the cells of the palisade and spongy parenchyma are some distance from the nearest sieve tube. Clearly, the tracheids which are carrying

a stream of water upward to the food-making cells can not well conduct the products of photosynthesis in the opposite direction. The transfer of sugar to the nearest sieve tubes is carried on by the border parenchyma cells. When the sugar reaches a part of the vein where there are sieve tubes, it is conducted by these elements to the larger veins, then to the midrib, and finally to the vascular bundles of the petiole, whence it passes into the phloem of the stem.

The Vascular Bundles.—It is easy to demonstrate that conduction, at least of water and of soluble carbohydrates, is carried on by the veins of the leaf. Water conduction by the veins can be shown by placing a leafy shoot in a water solution of some dye such as eosin. In a relatively short time the veins will be colored deeply by the dye which was present in the water conducted by the vascular bundles of the leaf to replace that lost by transpiration from the mesophyll. The demonstration of carbohydrate conduction by the veins is not so simple. Photosynthesis, when active, produces sugar more rapidly than it can be carried from the leaf. In such cases part of the sugar is changed into starch and stored in the mesophyll cells. If the chlorophyll is removed from such a leaf by means of alcohol, and the leaf then treated with iodine solution, the iodine acting on the starch gives the leaf a blue color. Such a test of a plant which has been in the dark for some time shows many of the formerly starch-filled leaves to have lost their starch, presumably by the starch being changed into sugar and conducted away. Cutting one of the main veins of a starch-filled leaf before placing the plant in the dark, in some cases prevents, or at least restricts, sugar movement from the part of the leaf traversed by branches of the cut vein, so that that part of the leaf retains its starch and colors blue with iodine. This demonstration frequently fails, however, presumably because when the vein is severed the sugar may be conducted around the gap, by the mesophyll cells.

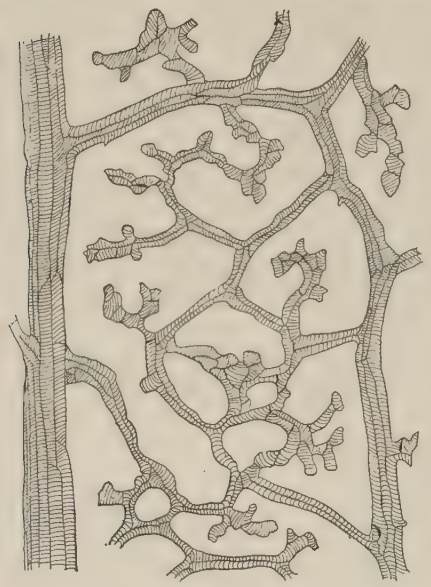


FIG. 155.—A portion of the vein system of a leaf. (Redrawn after Sachs.)

When a net-veined leaf is examined with a lens it can be seen that,

in addition to the veins which form the network there are still finer branches which end free, that is, are connected to other veins only at one end. There may be as many as 6000 of these minute vein endings in a square centimeter of leaf. They are made up of one or a very few tracheids surrounded by border parenchyma cells. The mechanical function of supporting the thin expanded sheet of epidermal and mesophyll tissue is performed principally by the large veins and the midrib. In the veins where phloem is present it occupies the lower side of the vascular bundle and the xylem the upper side. Groups of collenchyma cells or of bast fibers generally accompany the large veins and increase their strength and rigidity.

Anatomy of the Petiole (Fig. 156).—The petiole is sometimes cylindrical in form, but generally it is flattened or grooved on the upper side.

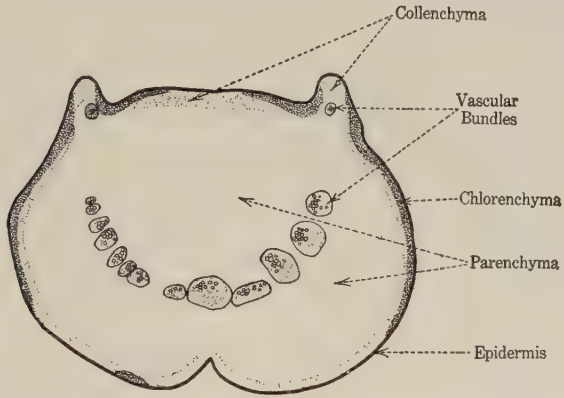


Fig. 156.—Cross section of the petiole of a potato (*Solanum tuberosum*) leaf.

The vascular bundles of the petiole are arranged, not in a complete circle as in the stem, but in a semicircle or C-formed line with the opening toward the upper side of the petiole. As in the vascular bundles of the leaf, the phloem occupies the lower part of the petiolar bundles and the xylem the upper part. The center of the petiole is usually made up of parenchyma cells. Tissues similar to those of the cortex of the stem are found outside the vascular bundles. In this region, collenchyma and bast fibers are often present but the starch sheath or endodermis is lacking. The form of the petiole and the arrangement of its mechanical tissues are such that it forms a relatively rigid support and yet permits the blade to yield to strong air currents.

The Absciss Layer, Leaf Fall, and Leaf Scars.—Leaf fall, in deciduous plants, occurs to a certain extent at all seasons but particularly at

the approach of winter. The conditions which favor leaf fall cause the cells near the lower end of the leaf stalk to become meristematic and to give rise to a zone of delicate, thin-walled cells extending clear across the base of the petiole. This is called the **absciss layer.** The middle lamella of these cells becomes changed chemically before leaf fall and the cells separate from one another with ease. When the wind, blowing against the blade of such a leaf, tends to cause the petiole to bend, the absciss layer is ruptured and the leaf becomes detached. When the absciss layer is formed the conducting elements of the vascular bundles generally remain unaffected, but they are not sufficiently

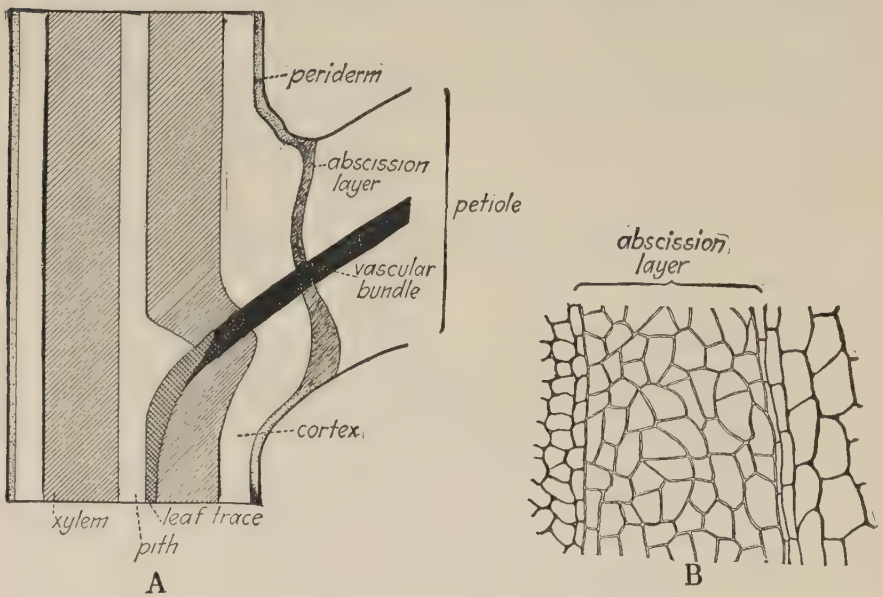


FIG. 157.—*A*, diagram showing leaf abscission layer; radial section through twig and leaf base in *Juglans cinerea*. *B*, detail of cellular structure of a small part of the layer three weeks before leaf fall. (From Eames and MacDaniels, *Introduction to Plant Anatomy*, McGraw-Hill Book Company.)

strong to prevent the fall of the leaf. Certain cells just below the abscission layer become lignified and suberized and form a protective coating over the part of the stem from which the leaf has separated. These areas, **leaf scars,** have been referred to in an earlier chapter (Fig. 6). Within each leaf scar the **bundle scars,** or broken ends of the vascular bundles which led from the petiole into the stem, may be seen. The form of the leaf scar and the number and arrangement of the bundle scars differ sufficiently in various deciduous plants to be used in distinguishing different genera and species in their winter condition.

THE PHYSIOLOGY OF THE LEAF

The primary functions of typical leaves, for which they clearly are specially adapted in form and structure, are photosynthesis and transpiration. In certain cases, some of which will be discussed later in this chapter, leaves carry on other (secondary) functions.

Photosynthesis.—The principal features of the process of carbohydrate manufacture by green cells were briefly stated in the chapter on the cell. Here we shall discuss this primary function of the leaf more fully. In our account we shall take up the following points in order: the raw materials, the energy factor, the by-product, the end-products, and finally the conditions influencing the process.

Raw Materials.—As we have learned, water and carbon dioxide are the raw materials of the photosynthetic process. The soil is the source of the water and the carbon dioxide is absorbed from the atmosphere surrounding the leaves. Though the atmosphere is not absolutely constant in its composition, the percentage by volume of its different components under natural conditions seldom varies much from the following figures:

	Per Cent
Nitrogen	78.2
Oxygen	20.8
Argon	1.0
Carbon dioxide	.03

Traces of ammonia, oxides of nitrogen, ozone, and other gases.

Each of these gases is present, therefore, in the intercellular spaces of the chlorenchyma. If the concentration of any one of these gases in the air within the leaf increases, some of that gas will tend to diffuse outward through the stomata. If there is a decrease in concentration of any one of the gases, that gas will tend to diffuse inward through the stomata from the air outside the leaf. All the gases of the atmosphere are soluble in water, though they differ greatly in solubility. Accordingly the surface film of water on the outside of the palisade and spongy parenchyma cells, where they are in contact with an intercellular space, as well as the cell sap of these cells, contains in solution a quantity of each of the atmospheric gases. The concentrations of any of these gases in solution in the cell sap, in the water of the surface film of the mesophyll cells, and in the intercellular air are interdependent. If one of these gases is being produced in the cell the concentration in the cell sap increases and as a result the concentration of that gas in the surface film and in the intercellular air also increases. Increase of that gas in the air within the leaf similarly affects its concentration in the

surface film and cell sap. Now, the process of photosynthesis removes carbon dioxide from solution in the cell sap. As a result there is diffusion of that gas inward from the surface film of water. The loss of carbon dioxide from this surface film is followed by its dissolving more carbon dioxide from the intercellular air, which thus has its carbon dioxide content lowered below that of the outside atmosphere. Diffusion of carbon dioxide inward through the stomata tends to make up the deficiency. Briefly stated, then, there is during photosynthesis a movement of carbon dioxide from the atmosphere outside the leaf to the interior of the green cells. The transfer of carbon dioxide may be considered as taking place in the following stages:

1. Passage by diffusion through the stomata into the intercellular spaces from the outside air.

2. Solution of more carbon dioxide from the intercellular air by the film of water on the surface of the chlorenchyma cells.

3. Diffusion through the cell wall and cytoplasmic membrane from the surface film to the cell sap to replace the carbon dioxide removed from solution by photosynthesis.

The water used by the green cells enters the root from the soil and is conducted upward through the xylem of the root and stem by processes which have already been discussed in the chapters on the root and the stem. In the leaf it passes along the petiole, midrib, and veins to the finest veinlets. None of the green cells are more than three or four cells removed from one of these small vascular strands. Water passes from the tracheids of the veinlets to the chlorenchyma cells by reason of the much greater concentration of the cell sap in those cells than of the solution in the tracheids. It passes first to the border parenchyma cells, whose cell sap is more concentrated than the watery solution in the tracheids. From the border parenchyma cells the water then passes to the green cells by reason of the greater concentration of their cell sap than that of the border parenchyma cells. The process of photosynthesis tends to maintain a high concentration in the cell sap of the green cells, both on account of the sugar which it produces and because of the water which the process removes from the cell sap. Transpiration from the green cells is, of course, more important in keeping the cell sap of these cells at a high concentration.

The quantity of carbon dioxide and water absorbed and converted into food and tissue by the plant is surprisingly large. A tree of moderate size may have a dry weight (weight of its tissue after removal of all water) of as much as 6500 kilograms. This is, of course, much less than the total weight of organic matter which the tree has produced, for during its life large quantities of food were respired, that is, converted

into carbon dioxide gas and water. Now, if we assume that 4 per cent of the 6500 kilograms of dry weight consist of nitrogen and other elements secured from the soil and 60 per cent is hydrogen and oxygen, we find that about 2500 kilograms of the weight of the tree was carbon. This is equal to the amount of carbon in the carbon dioxide of over 58,000,000 cubic meters of air or a volume 1 kilometer wide, 1 kilometer long, and 58 meters high. The water combined with this quantity of carbon is over 3500 kilograms, about 3500 liters. To make all the food produced by such a tree during its life, many times these quantities of carbon dioxide and water must have been utilized.

Measurements made by Brown and Escombe show that the common sunflower, when illuminated by diffuse sunlight, may absorb each hour in excess of 400 cubic centimeters of carbon dioxide per square meter of leaf surface. Under natural conditions very favorable for photosynthesis the sunflower leaf may absorb carbon dioxide at more than twice that rate (820 cubic centimeters per square meter per hour). That amount of carbon dioxide would be contained in an air column of 1 square meter cross section and $2\frac{1}{2}$ meters high.

The Energy Factor—Necessity of Light for Photosynthesis.—There are several interesting methods of showing that carbon dioxide and water can not be united to form carbohydrates in the absence of light. One of these depends upon the measurement of the dry weight of a given area of leaf tissue before and after a period of active photosynthesis. This method was first used by the great botanist, Sachs. Early in the morning of a warm sunny day he cut a given area from one-half of each of a number of leaves. This tissue he deprived of all of its water by heating to 100° C. until it lost no more weight. In the late afternoon he cut from the intact halves of the same leaves, an area of leaf tissue equal to that which had been taken in the morning. This leaf tissue he also deprived of its water. Upon comparing the dry weights he found that the tissue taken in the evening weighed more than that removed from the leaves in the morning. The difference represented part, but by no means all, of the material manufactured by the leaf surface in question during the day, for some of the sugar made was conducted away from the leaf and some was lost by respiration. If this experiment is repeated with plants which are kept in the dark during the day there will be no gain in dry weight. The conclusion is inevitable that light is essential to the increase in dry weight. Furthermore, it can be clearly shown that the increase in dry weight is due to the production of sugar and starch.

If we assume that the absence of starch in the green cells of the leaf is a safe indication that photosynthesis has not taken place, we can

easily show that photosynthesis will not go on unless light actually falls upon the green tissue. It is only necessary to keep a plant in the dark until its leaves have become emptied of starch, and then to place it in the light after covering one of its leaves with a mask of opaque paper or tinfoil with one or more openings cut in it. After some hours' exposure to light the leaf is removed from the plant, freed of its chlorophyll by means of alcohol, and treated with a solution of iodine. The portion of the leaf which was illuminated through the openings in the mask will take on the dark blue color which is characteristic of starch treated with iodine, while the remainder of the leaf will show no starch reaction.

A most conclusive and ingenious demonstration of the necessity for illumination, not merely of the green cells but of the chloroplasts themselves, is that devised by Engelmann. It rests upon the fact, already touched upon in the chapter on the cell, that oxygen is liberated from the cells in which photosynthesis is going on. Engelmann mounted an algal filament (one of the microscopic threads making up the green masses often seen growing in fresh-water pools or ponds) in water in which there were many motile bacteria. Then he sealed the edge of the cover glass to the slide with grease, so that no oxygen from the atmosphere might be absorbed by the water containing the bacteria and the algal filament. These motile bacteria are able to swim from place to place by reason of the rapid movements of their protoplasmic whips, or cilia. The movement of the bacteria is dependent on a supply of energy derived from their own respiration. Oxygen is necessary for respiration, and when the oxygen supply in the liquid surrounding them has been largely exhausted by their own respiration they lose their motility. Furthermore, they tend to move toward a region where that gas is more abundant.

When Engelmann's preparation of bacteria and of the algal filament (the latter consisting of green cells placed end to end) was kept in the dark, the bacteria soon came to rest on account of oxygen shortage resulting from their respiration and that of the algal cells. However, when light was allowed to fall upon the filament of green cells, many of the bacteria regained their motility and accumulated around the filament where oxygen was being liberated. Engelmann was able to project upon the alga a spot of light so small that he could at will illuminate a portion either of the chloroplast or of the colorless cytoplasm.

The bacteria accumulated about the filament only when the chloroplast itself was lighted. Engelmann thus showed not only that photosynthesis could not take place in the algal cells unless they were illumi-

nated, but that it was necessary that the light actually fall upon the chloroplast itself if photosynthesis were to go on.

The experiment just described shows that chlorophyll is essential to carbohydrate manufacture. Another convincing method of demonstrating this is by the use of variegated leaves, such as those of certain varieties of geranium (*Pelargonium*) and of *Coleus*, which have white bands or blotches. If the distribution of the non-green areas of such a leaf is carefully noted or sketched, it will be found when the leaf is treated with alcohol and then with iodine solution, after being exposed for some hours to light, that starch has not been formed in the parts where chlorophyll is absent.

The Energy Factor—The Function of Chlorophyll.—In order to understand the role played by chlorophyll in carbohydrate manufacture it is necessary to be familiar with some of the elementary facts in regard to the physics of that form of energy called light. There is a more or less general agreement that the energy of an electric current is due to electrons, particles of negative electricity in active movement, and that the energy of a hot body is due to rapid movement (with frequent impacts and rebounding) of its molecules; but as to the actual nature of radiant energy, including light, there are several theories, none of which has found general acceptance. According to one theory, visible light consists of waves or vibrations varying in amplitude (wave length) but all capable of perception by the human eye. These waves generally originate in some hot body such as the sun or other stars, the incandescent filament of an electric light bulb, or the hot carbon particles of a gas or oil flame. Since light can pass through spaces where there is no matter, there has been assumed the existence of a medium called " the ether " which is without the characteristic properties of matter but exists everywhere and is able to transmit light waves. The ether theory, though no longer accepted by many physicists, is the most easily understood of the various theories of light and makes it possible to explain certain observed facts which are not explainable by other theories. White light is made up of ether vibrations or waves of different lengths, ranging from the relatively long waves of red light, through the successively shorter waves of orange, yellow, and green light to the very short waves of blue and violet light. The wave lengths of visible light range from about 7/10,000 millimeter in the extreme red through orange, yellow, green, blue and indigo to about 4/10,000 of a millimeter in the extreme violet. By means of a glass prism and other devices a shaft of white light can be resolved into its component colors. In the resulting band of color, which is called the **spectrum,** the different component colors of white light are arranged in the order of their wave

length. Beyond the end of the visible spectrum at the red end, are still longer waves which our eyes are incapable of perceiving. These are spoken of as infra-red light. Beyond the violet end are shorter waves, also invisible, which are called ultra-violet light. Such ether waves of whatever length and whether visible or not are spoken of collectively as radiant energy. The term includes the waves, up to hundreds of meters in length, by means of which wireless messages are transmitted and the extremely short waves of the so-called X-rays.

When white light falls upon a white object all the different component colors are reflected to the eye. When a white object is illuminated by red light or by blue light the object appears red or blue because of the reflection to the eye of the colored light which falls upon it. Dead black material, like black velvet, absorbs practically all the light

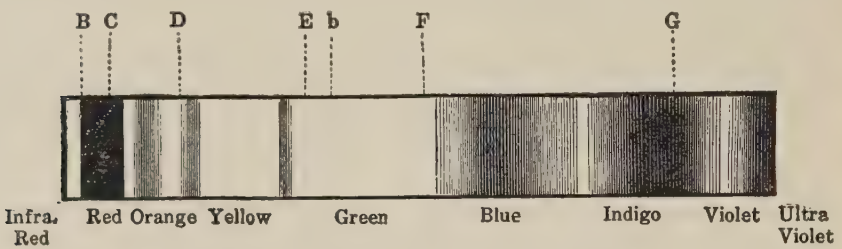


FIG. 158.—Absorption spectrum of a chlorophyll solution, extracted from green leaf. (From Kraus.)

which falls upon it regardless of whether it is white light or colored light. It is black merely because it reflects no light to the eye. Colored materials absorb certain of the components of white light which falls upon them and reflect others to the eye. Thus a piece of green paper absorbs most of the light which falls upon it except the waves of green light, which it reflects. This last statement must be somewhat qualified. Strictly speaking green light is light of a certain range of wave lengths, between 50 and 55 hundred thousandths of a millimeter. The eye, however, perceives as green not only such mono-chromatic light but also mixtures of longer wave lengths (yellow light) and shorter wave lengths (blue light) even though green light is entirely absent. The light absorbed by black or other colored material is largely converted into heat energy.

The green color of chlorophyll indicates, at least, that that pigment reflects much of the green component of the light falling upon it, and absorbs the other kinds of light at least in part. It is possible to determine what part of the white light is absorbed by chlorophyll, and then

permit the light which has passed through the solution to fall upon a glass prism so that it is broken up into its component colors. In place of an alcoholic solution of chlorophyll we may use a leaf, the intercellular spaces within which have been filled with water to render it less opaque. The resulting spectrum will be found to be different from that of white light which has not passed through a chlorophyll solution or a green leaf. It will lack a considerable part of the red and much of the blue, indigo and violet. Part of the red and most of the yellow, orange, and green are only slightly changed by passage through the chlorophyll. Thus we learn that it is a certain part of the red and some of the blue, violet, and indigo which are absorbed from white light when it passes through the leaf. That particular part of the red region of the spectrum (from about 60 to 65 hundred thousandths of a millimeter) which is absorbed is absorbed almost completely, in solutions of moderate concentration, while there is only partial absorption of the blue, violet, and indigo. Amount of absorption changes with the thickness of the layer and the concentration of the solution and if the concentration is very great and the layer very thick the green light is absorbed.

The Energy Factor—Evidence of the Relative Effectiveness of Different Parts of the Spectrum.—We have already learned (Chapter on The Cell) that the production of carbohydrates from carbon dioxide and water is an energy-absorbing process, that is, a process which can go on only if energy is continuously supplied from without. In previous paragraphs it has been shown that light is the only form of energy which green plants can use for this process. Now it is clear that the light which the leaf does not absorb can not be used in photosynthesis, but it does not follow that the violet, indigo, blue, and part of the red which are absorbed are all suitable as sources of energy for that process, nor does it follow that the relatively small amounts of green, yellow, and orange light which are absorbed can not be used in photosynthesis. Only experiment can answer the questions as to what part of the absorbed light can be used in carbohydrate manufacture. One of the most direct methods is to project a spectrum upon a starch-free leaf which receives light from no other source, and then after a time remove the leaf from the plant and treat it with alcohol and with iodine solution. It will be found that where the orange, yellow, and green light fell upon the leaf there is little or no evidence of starch formation, but that abundant starch is present where the leaf was lighted by the blue end of the spectrum and by that portion of the red in which the absorption by chlorophyll is most complete.

By the use of his method (already described) of mounting motile bacteria, together with an algal filament, under a cover glass sealed to

the slide, Engelmann also demonstrated that all the different components of white light which are appreciably absorbed by chlorophyll are active in photosynthesis. He found when he cast a very small spectrum lengthwise upon the algal filament that the bacteria accumulated in large numbers around the filament where it was lighted by the blue end of the spectrum and by the intensely absorbed portion at the red end (Fig. 159) The aggregation of these motile bacteria in the red part of the spectrum was much greater than at the blue end, indicating that oxygen liberation and therefore photosynthesis were most active in the region of most complete absorption.

Since Engelmann's time this subject has been studied by much more exact methods than his and the most recent results seem to show that the shorter the wave length the less effective it is in photosynthesis. It appears also that there is no relation between amount of absorption of a light of given wave length and its effectiveness in photosynthesis. Although photosynthesis is more active in the red, where absorption by chlorophyll is intense, than in the green, where there is little absorption by chlorophyll, the effectiveness of green light is greater than the light which is absorbed to a much greater extent than the green.

Efficiency of the Leaf in Utilizing Sun's Energy.—Inasmuch as all the energy available for use in our own bodies, as well as most of that used in the industries, is solar energy originally absorbed and stored by green plants, the efficiency of the leaf in fixing the radiant energy of the sun is a matter of particular interest. The following table gives the principal results of one series of measurements of the efficiency of leaves in energy absorption which was made at Cambridge, England. It must be borne in mind that the values would vary considerably according to the species, the age of the leaf, the intensity of the sunlight and other factors. In this experiment the leaves were exposed to full sunlight. Variegated leaves were used and the energy quantity absorbed by the chloroplasts was determined by subtracting that absorbed by white portions of the leaf from the quantity absorbed by green portions.

	Per Cent
Total energy of sunlight falling on upper leaf surface	100
Energy absorbed by green part of a variegated leaf	80
Energy absorbed by chlorophyll-free part of such a leaf	70
Energy absorbed by the chloroplasts of the green part of the leaf.	10
Energy actually utilized in photosynthesis	3.5

It is clear from this table that under the conditions of this particular set of experiments about 35 per cent of the energy actually absorbed by the chloroplasts or 3.5 per cent of all the light energy falling on the leaf was used in photosynthesis. The part absorbed by the leaf but not

used in sugar manufacture (in this case about 76.5 per cent of the total energy) may raise the temperature of the leaf and then be in part transferred to, and raise the temperature of, the surrounding air. At times, when the temperature of the surrounding atmosphere is high, and loss of heat from the leaf to the air slow, this energy may cause the tissue of the leaf to reach a relatively high temperature. It may be that fatal heating of the protoplasm might thus result, were it not for the fact that the conversion of water into water vapor during transpiration absorbs large quantities of heat energy and thus keeps down the temperature of the leaf. In general, the average efficiency of green plants in the utilization of sunlight falling upon their leaves is probably much less than the values given above, perhaps as low as 1 per cent.

The By-product.—The equation which has been used to express in simple form the chemical changes which take place during photosynthesis ($6CO_2 + 6H_2O = C_6H_{12}O_6 + 6O_2$) shows that oxygen is freed during the process. This gas is an incidental product or by-product of photosynthesis and its production is clearly not to be considered as the object of the process, for the green cells from which the gas is liberated are in constant and direct contact with the intercellular air of the leaf, which normally contains a large proportion of oxygen.

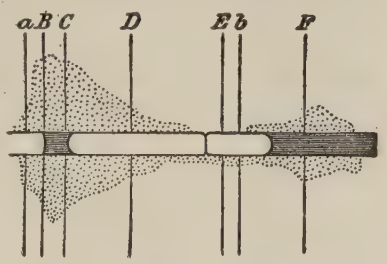


FIG. 159.—Diagram illustrating Engelmann's experiment demonstrating the regions of the spectrum most active in photosynthesis. See text for an account of this experiment. In this diagram the algal filament is shaded to show the portions which are lighted by the parts of the spectrum most strongly absorbed by chlorophyll. The dots represent the bacteria which accumulate where oxygen is relatively abundant. The lettered vertical lines show the position of certain dark lines characteristic of the solar spectrum and serve here merely to indicate different regions of the spectrum. (From Palladin, after Engelmann.)

That some gas is liberated by green plants during photosynthesis is shown by the bubbles which are constantly being given off by submerged water plants while they are lighted by the sun. In the case of the filamentous, fresh-water algae which are often called "pond scums," the accumulation of these bubbles of gas among the filaments causes the masses of algae to float at the surface of the water when brilliantly illuminated for any length of time. If an inverted glass funnel is placed in water over a mass of green algae or other green water plants and the stem of the funnel is filled with water and then closed, the gas given off by the plants may be collected. After a considerable quantity

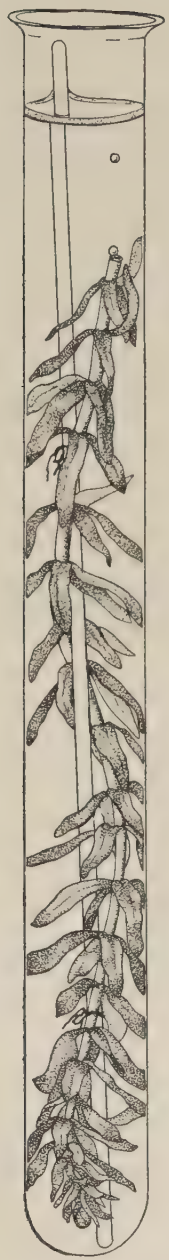


Fig. 160.—A branch of the immersed aquatic plant, *Elodea*, showing the liberation of bubbles of oxygen (a by-product of photosynthesis) when the plant is illuminated. See text.

has accumulated it may be tested by opening the funnel tube and holding a glowing splinter in the stream of gas which is expelled. The live coal will burst into flame, an indication that the gas is largely oxygen.

If a green leaf be placed in a gas-tight glass vessel with air containing a known quantity of carbon dioxide and then exposed to sunlight, it can be shown after a time, by analysis of the air, that there has been an increase in oxygen and a decrease in carbon dioxide. The volume of carbon dioxide absorbed by the leaf is almost exactly equal to the volume of oxygen liberated by the leaf. Since, according to Avogadro's Law, equal volumes of different gases under like conditions of temperature and pressure contain the same number of molecules, we can conclude that for every molecule of carbon dioxide absorbed by the green cell during photosynthesis one molecule of oxygen is liberated. Thus our equation for this process is supported by experimental data.

We have already seen how oxygen liberation was employed by Engelmann in his "bacterium method" as a measure of the rate of photosynthesis. The "bubble method" for comparing the rate of photosynthesis under different external conditions also utilizes oxygen liberation as a measure of rate of photosynthesis. If a stalk of some small aquatic plant, such as water weed (*Elodea*), water milfoil (*Myriophyllum*), or hornwort (*Ceratophyllum*) is cut off, loosely attached in an inverted position to a glass rod (Fig. 160) and immersed in a test tube, bubbles of oxygen will be given off at fairly regular intervals from the cut end, if the plant is illuminated. The number of bubbles produced in a given time is approximately proportional to the rate of photosynthesis. Lowering the temperature greatly, very much increasing it, or lessening the intensity of the illumination, will decrease the rate at which bubbles are formed. Bubble formation will cease if the plant

be placed in water which has been deprived of carbon dioxide by boiling and subsequently cooled to its original temperature. Removal, by means of a light screen, of the red and blue from the light falling upon the plant will also greatly reduce the number of bubbles formed in a given period of time.

Whereas photosynthesis goes on only during the period of daylight, respiration continues during both day and night. Respiration involves the absorption of oxygen and the liberation of carbon dioxide. However, in a plant which is actively growing or accumulating food reserves, the amount of oxygen liberated into the atmosphere by photosynthesis during the twenty-four hours is considerably in excess of that absorbed by respiration, and the carbon dioxide contributed to the atmosphere by the respiration of such a plant is much less than that absorbed during photosynthesis. It is important to man and to other animals that the concentration of oxygen in the atmosphere be kept fairly uniform in order that their respiration may continue at the accustomed rate. Furthermore, an accumulation of carbon dioxide in the atmosphere would sooner or later interfere with their life processes. Therefore, since they are not able, as are green plants, to add oxygen to the atmosphere, or to remove carbon dioxide from it, the power of green plants to " purify " the " vitiated " atmosphere, by removing carbon dioxide from it and adding oxygen, is of considerable significance.

Ganong has computed that approximately 25 square meters of green leaf surface will give out, during a moderately warm and sunny summer day, the quantity of oxygen used by a man for respiration during the same period. However, since man's respiration continues at night and during the winter, it would require about 150 square meters of leaf to supply to the air during the summer the quantity of oxygen used by a man during the year.

The End-products.—In most plants the first visible product of photosynthesis is starch. In *Vaucheria,* one of the filamentous, freshwater algae, oil is the first product which appears, starch never being formed. It has been reported that in many of the Musaceae (banana family), starch is absent from the leaves, oil being instead the first visible product of photosynthesis; and in many other monocotyledons there is no visible product of that process to be found within the green cells, for the sugar produced remains in solution.

The sugar which is the immediate product of photosynthesis has been generally assumed to be glucose ($C_6H_{12}O_6$). There is some evidence, however, that it may be sucrose (cane sugar) ($C_{12}H_{22}O_{11}$). Both of these sugars are present in considerable quantities in plants. Detached leaves kept in the dark and supplied through their petioles with various

sugars are able to convert the sugars into starch. Among sugars which may be thus utilized for the production of starch in the absence of light are milk sugar (lactose), cane sugar (sucrose), malt sugar (maltose) and grape sugar (glucose).

The Course of the Process.—There have been many attempts to determine the steps by which glucose or sucrose (cane sugar) is built up from carbon dioxide and water. One suggestion which has been put forward is that from the raw materials (CO_2 and H_2O) formaldehyde (CH_2O) is first formed, and that six such molecules are then built up to form a single glucose molecule ($C_6H_{12}O_6$), or that twelve formaldehyde molecules are united to form, after the loss of one water molecule, a molecule of cane sugar ($C_{12}H_{22}O_{11}$). It should be stated, however, that the question of the actual course of the chemical reactions involved in carbohydrate manufacture is still an open one.

Rate of Carbohydrate Production.—The amount of carbohydrate produced by a given area of leaf in a given time varies greatly in different plants and under different external conditions. Experiments carried out with leaves of the sunflower (*Helianthus*) show that a square meter of leaf surface may in the course of a summer's day produce as much as 25 grams of starch.

Conditions Influencing the Rate of Photosynthesis.—Under natural conditions the rate of photosynthesis is determined by three factors. These are:

1. Temperature.
2. Intensity of the illumination.
3. Carbon dioxide content of the atmosphere.

The lowest known temperature (minimum) at which it is possible for photosynthesis to go on is several degrees below the freezing-point of water. For plants of the temperature zone the optimum temperature (heat intensity most favorable) for the process is about 37° C. and the maximum (temperature above which the process ceases) from 43° to 45°.

The amount of material produced by a given area of leaf surface increases with the increase of illumination up to a certain point (the optimum light intensity) if the temperature and the carbon dioxide supply are sufficient.

Although under natural conditions optimum illumination and temperature exist for considerable periods, green leaves do not during such periods produce the greatest quantity of carbohydrates which they are capable of producing. The .03 of a per cent concentration of carbon dioxide in the atmosphere is far below the optimum. At ordinary temperatures and with moderate illumination, artificial increase of carbon dioxide up to a concentration of .25 of a per cent results in increased

carbohydrate production. Further increase in carbon dioxide does not increase photosynthesis unless the illumination, or the temperature, or both are increased. It was shown at Cambridge, England, that at a temperature of 30° C., and even with an excess of carbon dioxide, a sunflower leaf required only about seven-tenths of the full sunlight of an

Fig. 161.—A potometer for measuring the rate of transpiration of a shoot. As the leaves transpire more water is drawn into the shoot from the potometer. This results in a current of water passing from right to left in the horizontal capillary tube. If the vial of water at the right is removed for a short time a bubble of air enters the capillary. This will be carried along the capillary tube by the water current, its rate of movement being a measure of the transpiration rate. The bubble may be caused to move in the reverse direction by admitting water from the glass reservoir tube just above the support. (Cut loaned by the Bausch & Lomb Optical Company.)

August day in order to produce carbohydrates at the maximum rate. This value would vary, however, according to the species and the varying quality and quantity of " full sunlight " on different days and in different localities.

Under favorable natural conditions of illumination and temperature, the carbon dioxide content of the atmosphere is, then, the limiting factor for photosynthesis. That is to say, at the temperature of a sunny day during the active, growing season, the amount of carbohydrate produced could not be increased by rise of temperature or increase of illumination, but only by increase of carbon dioxide concentration above that normally present in the atmosphere. If we wished to make it possible for a sunflower plant to manufacture the greatest possible quantity of carbohydrate in a given period we should take the following measures: (1) artificially maintain a temperature of about 37° around the plant; (2) illuminate it continuously with that light intensity (at least equal to full sunlight) which experiment proved to be the optimum; and (3) artificially increase the quantity of carbon dioxide to the optimum (somewhere above .25%). It is not practicable to maintain the temperature and illumination to which field or garden crops are subjected at the optimum. Over limited areas in the vicinity of certain European industrial plants, which produce carbon dioxide as a by-product, increase of the quantity of carbon dioxide in the atmosphere in which a crop is growing has been attempted, and is said to have resulted in an increase in yield.

The Utilization of the Product of Photosynthesis.—The sugar, glucose, which is believed to be the immediate product of the photosynthetic process, constitutes the foundation material out of which many other plant substances are built up. Part of this carbohydrate is respired, some of it is stored as cane sugar or starch in various tissues of the plant, but a very large portion is transformed chemically into various substances which play a part in the life of the plant. We may classify these substances as follows: (1) Those which compose the plant skeleton; (2) reserve foods; (3) living protoplasm, and (4) various secretions.

Part of the sugar is converted into cellulose for the formation of the walls of new cells and for the thickening of old walls of living cells. The reserve foods of which glucose forms the basis are principally (1) **carbohydrates,** such as the sugars (such as fructose, sucrose), starches and hemicellulose, (2) **oils,** and (3) **proteins.** The carbohydrates and oils contain the same elements, carbon, hydrogen and oxygen, found in the glucose molecule; consequently, the chemical transformation of glucose to these substances does not involve the addition of other elements. But, in the building of proteins, the elements, nitrogen, sulphur and phosphorus, are added to those of the glucose, the stages in this chemical process being complicated. Probably, the formation of proteins may take place in any part of the plant but in some plants protein manufac-

ture has been shown to be particularly active in the leaves. Living protoplasm, as has been stated, is a complex mixture of a number of substances, chiefly proteinaceous in character.

Of the various substances produced in plants the following may be mentioned: (1) the **essential oils,** such as lemon oil, cedar oil, clove oil, and other volatile oils which are capable of imparting odors to fruits and flowers and other parts of the plant; (2) the **resins,** which are particularly abundant in pines; (3) **latex,** a milky secretion; the latex of certain plants is the basis of rubber; (4) various **pigments,** such as chlorophyll, xanthophyll, carotin and anthocyanin; (5) **alkaloids,** nitrogenous compounds, such as quinine (from the bark of *Cinchona* tree), caffein (from coffee), thein (from tea), morphine (from the poppy); (6) **glucosides,** substances which on decomposition give rise to some kind of sugar together with certain aromatic substances; examples of glucosides are **amygdalin** which is found in the seeds of the bitter almond and other nuts, and **sinigrin** found chiefly in the seeds of mustards; (7) **enzymes,** complex protein compounds, which act as organic catalysts in the plant; (8) **acids,** such as malic acid (from the apple), and citric acid (from citrus fruits), and (9) **tannins,** substances which impart an astringent, bitter taste to tissues which possess them.

Transpiration.—If a bell jar, or other large glass vessel, be placed over a potted plant, fine drops of water will soon make their appearance on the inner surface, and these will finally collect into larger drops and run down the glass walls. Evidently the air within the chamber has been receiving from some source a quantity of water, part of which has become condensed upon the glass. If the possibility of water passing into the air by evaporation from the soil in the pot is excluded by sealing the pot and the soil surface with paraffine, the results of the experiment are unchanged. The conclusion to be drawn is that water passes from the aerial parts of plants into the surrounding air.

As a matter of fact, all the higher plants, except such submerged forms as water weed (*Elodea*) and water milfoil (*Myriophyllum*), are constantly losing water, which passes into the atmosphere in the form of water vapor. This process is called **transpiration.** Another method by which it may be demonstrated, and at the same time accurately measured, is by the use of a balance. If a potted plant, with the pot and soil surfaces sealed with paraffine or completely enclosed in sheet rubber or other waterproof covering, is placed on the scales and accurately weighed, it will be found after a short interval that the plant has lost weight. Successive weighings will show that it continues to lose weight. If the plant were kept in the dark between weighings, the loss in weight would include that due to respiration as well as that resulting

from transpiration, but the resulting error in transpiration measurement would not be large in an actively transpiring plant. The weight loss might be somewhat less than the weight of water transpired if the plant were kept in the light between weighings, for the plant might well gain by photosynthesis more than it lost by respiration.

Though related to evaporation, such as takes place from a water surface or from a wet cloth, transpiration is different in that it is controlled in part by the plant itself. The rate of water loss (by transpiration) from a living plant is less than the water loss (by evaporation) from a dead plant.

Utility to the Plant.—It was formerly the general belief that the inorganic salts from the soil were carried into the roots with the absorbed water, and that therefore the quantity of these salts which entered the plant depended upon the quantity of water absorbed. There is, however, no apparent reason why substances in solution in the soil water should not diffuse into the root hairs even though there is no simultaneous absorption of water. It has recently been shown by experiment that reduction of the quantity of water absorbed by a plant does not proportionally reduce the quantity of soil solutes absorbed. In these experiments water absorption was reduced by cutting down the rate of transpiration. According to one investigator, " if there is a definite relation between the quantity of water transpired and the quantity of salts absorbed, one would expect that doubling the transpiration in plants would considerably increase the absolute weight and percentage of ash in plants. This is not the case." It is therefore very questionable whether transpiration plays an important rôle in increasing the absorption of essential mineral substances from the soil.

The great surface exposed by the leaves of a typical plant is favorable to the absorption of large quantities of carbon dioxide and of light energy for photosynthesis. It subjects the plant, however, to the danger of transpiration exceeding water absorption, a condition which results in wilting, or, if long continued, in the death of the plant. The question naturally suggests itself as to whether the large water loss through transpiration is merely an unavoidable result of the development of a great leaf surface by the plant or is a process which plays a useful rôle in the life of the plant.

Transpiration and the Transpiration Stream.—In the chapter on the stem, the withdrawal of water from the conducting tissues of the leaf by the mesophyll cells was given as the principal factor in maintaining the stream of water and soil solutes from the root to other parts of the plant. It is this osmotic pull upon the water in the tracheids of the veinlets which is responsible for drawing the weak solution in the

veins and vascular bundles of the stem upward. The water drawn into the mesophyll cells tends to reduce the concentration of their cell sap. As a result, those cells would lose their power to draw water from the veinlets, the upward stream would cease or at least be greatly reduced, were it not for the fact that the mesophyll cells are losing water by transpiration at the same time that they are withdrawing water from the veinlets. Transpiration can, then, be said to be the main condition determining the movement of water, and possibly essential minerals also, from the roots to the leaves. Although a large part of the energy of the sunlight which falls upon a green leaf is absorbed by it, a relatively small part of it is actually used in photosynthesis. The greater part of that absorbed is already in the form of heat or is transformed into heat within the leaf. As a result, temperatures very injurious, or even fatal, to the protoplasm might exist within the leaf during periods of exposure to very bright sunlight, were it not for the cooling effect of transpiration. The student should distinguish clearly between temperature and heat quantity. In an earlier chapter it was pointed out that the unit of temperature (heat intensity) is 1° C. which is the one-hundredth part of the difference in heat intensity of pure water at the freezing-point and at the boiling-point. The unit of heat quantity is the **calorie** which is the quantity of heat necessary to increase the heat intensity (temperature) of one gram of pure water 1° C. A kilogram of water and a gram of water at 50° C. have the same heat intensity but the first has 1000 times the heat quantity of the single gram of water.

Among the remarkable properties of water are two which fit it particularly well to protect the plant from excessive heating. First, is its great power of absorbing large quantities of heat without great increase in temperature. A calorie of heat raises the temperature of one gram of water only one degree. A calorie would raise the temperature of most liquids much more, of mercury, for instance, 30°. Since protoplasm contains so large a percentage of water it shares this tendency of water to "keep cool." Second, when water changes into water vapor a large quantity of heat must be absorbed—over 500 calories for each gram of water. When the water evaporates in the transpiring plant these hundreds of calories will be absorbed in part from the leaf, if it is at a high temperature, and thus the leaf may be cooled. The change of water from the liquid to the gaseous form in transpiration is a process which absorbs large quantities of heat from the tissues if the latter are at a high temperature. The quantity of heat necessary to change a given quantity of water to water vapor without changing its temperature is over five times the heat necessary to raise the tem-

perature of the same quantity of water from the freezing-point to the boiling-point. The absorption of this large quantity of heat from the leaf as water is transpired is believed to cool the leaf in somewhat the same way that the evaporation of perspiration from the human body tends to lower its temperature.

Conditions Affecting Transpiration Rate.—The amount of water lost by transpiration depends upon (1) **external factors,** conditions outside the plant and (2) **internal factors,** conditions in the plant itself.

External Factors.—In measuring the effect of external conditions upon the rate of transpiration, the balance may be used to show, by the change in weight of a plant, the quantity of water lost.

The principal external factors which affect the transpiration rate are the following:

1. Humidity of the atmosphere.
2. Light intensity.
3. Air movements.
4. Air temperature.
5. Soil conditions.

Humidity of the Atmosphere.—The less moisture there is in the air surrounding the plant the greater will transpiration tend to be. Though water loss is very slight in a water-saturated atmosphere it has been shown that it does not cease entirely. When plants which have been absorbing and transpiring water actively have transpiration suddenly checked while intake of water continues, drops of water may come out of the tissues. This can be shown by inverting a large tumbler over a flower pot in which young oat or wheat plants are growing. If the plants have been well supplied with water and have been previously exposed to warm, dry air, drops of water will appear on the leaves and often increase in size until they fall off or run down the leaves. This exudation of water in the liquid form under the conditions described is called **guttation.** It takes place in various plants during moist, cool nights following warm summer days. Many plants possess special structures (sometimes stomata), called **hydathodes,** through which water of guttation is allowed to escape.

Light Intensity.—Illumination has a marked effect on water loss by transpiration. Wiesner found in his experiments upon this subject that a plant of Indian corn gave off from each 100 square centimeters of its surface 97 milligrams of water per hour while in the dark, 114 milligrams in diffuse sunlight, and 785 milligrams in full sunlight. Illumination may increase transpiration in two ways: (1) by causing the guard cells to open the stomata widely, and (2) by raising the temperature of the leaf.

Air Movements.—When the air surrounding the plant is quiet, it becomes almost saturated with water vapor because of transpiration and the slowness with which the water vapor diffuses away from the leaf. This "moist blanket" of air naturally checks transpiration. Movement of the air sweeps away this mantle of moist air and brings fresh and drier air to the surface of the leaves, and as a result transpiration increases.

Air Temperature.—In general, experiments show that, other conditions remaining constant, transpiration increases with rise and decreases with lowering of the temperature of the surrounding air.

Soil Conditions.—When transpiration has been for some time more active than water absorption, the plant shows that it is suffering water shortage by beginning to wilt. It is believed that the rate of transpiration is not influenced by the soil moisture content until the soil reaches approximately the wilting coefficient. Although it has been shown that the stomata may remain open for some time after wilting begins, there is a large reduction in transpiration rate as soon as wilting begins. The mesophyll cells give up water vapor much less freely when they are in a condition of water shortage than when they are abundantly supplied with water. This results whether the water shortage is due either to excessive transpiration or to restricted water absorption. Accordingly, any soil conditions which affect the rate of water absorption will also change the rate of transpiration.

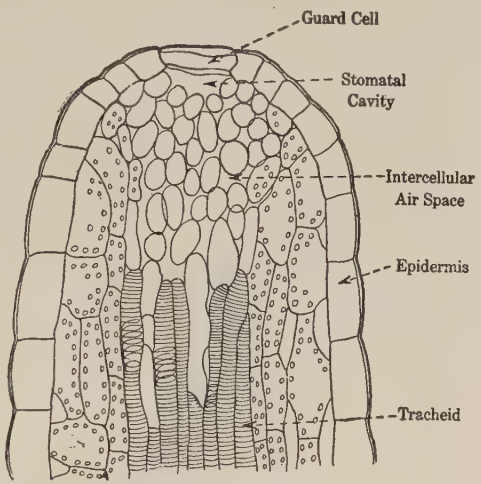


FIG. 162.—Longitudinal section through a marginal tooth of a leaf of Chinese primrose (*Primula sinensis*), showing the structure of a hydathode. Not a few plants, particularly those of humid regions, possess these special structures which excrete water in the liquid form during guttation. (Redrawn after Haberlandt.)

Internal Factors.—*Means of Reducing Transpiration.*—All flowering plants, with the exception of a few submerged aquatic ones, have provisions for regulating transpiration. If this were not so, even in the case of a plant provided with abundant soil moisture and living in a

very moist atmosphere, a short period of relative atmospheric dryness, such as would result from a sudden rise in temperature, might cause serious injury or death. This would result from a failure of the roots to absorb, or of the vascular bundles to conduct, sufficient water to replace that lost by transpiration.

Through the layer of cuticle forming the surface of all mature leaves, some water does escape into the air. This loss of water through the cuticle is spoken of as **cuticular transpiration,** to distinguish it from water loss through the stomata which is called **stomatal transpiration.**

The principal means by which the plant is able to reduce cuticular transpiration are the thickening of the outer wall of the epidermal cells, the presence of large quantities of the wax-like material, **cutin,** in this wall, and the production of close-set rods of wax (the so-called " bloom " which occurs on many fruits, leaves, and stems and has the appearance of a very fine powder). The leaves of pinks, or carnations, possess a blue-gray coating of wax, or " bloom," which may easily be wiped off. The amount of cuticular transpiration is very much less than that of stomatal transpiration.

The following brief table gives the average number of stomata per square millimeter on the upper and lower surfaces of the leaves of some common plants:

Name of Plant.	Average Number of Stomata per Square Millimeter.	
	Upper Surface.	Under Surface.
Apple (*Pyrus Malus*)	0	250
Olive (*Olea europaea*)	0	625
Pea (*Pisum sativum*)	101	216
Rubber plant (*Ficus elastica*)	0	145
Corn (*Zea mays*)	94	158
Barberry (*Berberis vulgaris*)	0	229

Clearly the stomata on the under surface of the leaf will be less likely to endanger the plant by allowing excessive transpiration than would stomata on the upper surface. The temperature of the lower, and therefore shaded, side of the leaf will be less than that of the upper side when the sun is shining brightly, and the air adjacent to the lower surface of the leaf will not tend to be so dry as that next to the upper side of the leaf.

Leaves which hang straight down, like those of some poplars and the adult leaves of eucalyptus (Fig. 153), have about the same number of stomata on the two sides. The same is true of leaves, like those of many grasses, which stand almost or quite perpendicular. In the case of a few plants, such as those water lilies whose leaves float on the surface of water, there are no stomata on the lower leaf surface.

Stomatal transpiration is sometimes reduced by depression of the stomata below the general surface of the leaf. In plants with such sunken stomata, gases have to pass through an outer chamber formed by overhanging epidermal cells, or, as in the tropical palm, *Nipa fruticans* through a tortuous passage, before entering the stoma (Fig. 149). By this means the transpired water vapor is prevented from being swept away from the stoma at once by air currents, and transpiration is reduced.

Most plants are able, by opening or closing the stomata, to alter greatly and quickly the water loss due to transpiration. On page 194 a brief account was given of the mechanism by which the guard cells open and close the pore (stoma) between them. In general it may be said that leaves reduce water loss by closing the stomata whenever there is no necessity for carbon dioxide absorption. The guard cells generally react promptly to a change from light to darkness or from darkness to light, closing the stoma in the former case and opening it in the latter.

In the willows (*Salix*) the guard cells have lost their power of regulating the stomata and the latter remain permanently open. It may be largely on this account that the willows are generally restricted to habitats where there is abundant water in the soil.

Other Methods of Reducing Transpiration.—In some plants, certain grasses, for example, transpiration, both stomatal and cuticular, is reduced, when water shortage begins, by rolling of the leaves. By this method the leaf surface exposed to light and to the dry atmosphere is reduced.

It is commonly assumed that the presence of epidermal hairs reduces transpiration. Of this there is some question, especially in cases where the hairs are made up of living cells. Experiments with some plants have shown that the water loss from the leaves is greater when the hairs are present than when they are lacking. It is unsafe to make a general statement as to the effect of epidermal hairs on transpiration.

Many plants living in places where the water supply in the soil is small and the atmosphere very dry, reduce both stomatal and cuticular transpiration by having very small leaves, by shedding the leaves soon after they are formed, or by producing no leaves at all. In either of the two latter cases the stems perform the typical leaf functions. Clearly

such provisions for restricting water loss result in a great sacrifice of photosynthetic activity.

Respiration in Leaves.—As we have already learned, the oxidation of food into carbon dioxide and water, with the liberation of the energy which was stored in the molecules of the food substance, is a process going on in all living cells. It is particularly active in the growing parts of the plant and in the leaves and flowers. Part of the energy liberated by respiration is in the form of heat. Under natural conditions this heat does not cause any considerable rise in the temperature of the leaf, for it is quickly dissipated into the surrounding air. However, if many fresh green leaves are piled together, the center of the mass soon becomes very warm, since the heat liberated by their respiration can not readily escape. Molisch found that in the center of a large pile of pear leaves a temperature of 44° C. above that of the surrounding atmosphere was attained within a little over twenty-four hours.

Special Functions Sometimes Performed by Leaves.—Besides the primary functions of photosynthesis and transpiration, and those of growth and respiration, the leaves of various plants may perform certain special functions in the service of the whole plant. In some cases the leaves that are adapted to carry on such special functions continue actively to transpire and to manufacture food, but in other cases their adaptation to perform a special rôle in the life of the plant is attended by loss of the primary functions. Examples of such special functions are protection (bud scales and leaf spines), food storage, water storage, attachment (tendrils), and capture of insects for food.

Protection—Bud Scales.—We have already learned that the delicate growing point, or primordial meristem, within the buds is surrounded and protected by the overlapping rudimentary leaves which later develop into typical foliage leaves. Except in those species which live in very moist, warm habitats where there is little danger of injury from dry air or low temperature, the rudimentary foliage leaves of perennial woody plants and the other parts within the buds are protected by scale leaves called bud scales.

These are generally small, brown in color, and rather tough in texture. They are often covered with dense hairs on the outer surface. In the poplars and many other plants they secrete a resinous substance which makes the scale covering of the buds water-proof. The bud scales originate as lateral outgrowths of the growing point, as do the foliage leaves. That they really are modified leaves or leaf bases is clearly indicated by the various structures intermediate between typical bud scales and typical foliage leaves which can be found in buds of horse chestnut (*Aesculus*), certain maples (*Acer*), and many other woody plants.

Protection—Leaf Spines.—Leaves are sometimes entirely or in part transformed into spines. In cactus, for example, these spines certainly protect the plants from destruction by browsing animals, although we are scarcely justified in saying that they have been developed by the plant in order that they might furnish this protection. Such spines are found on many desert plants, and if these plants were not so armed they would be very liable to destruction by animals for the sake of the stored water which they contain. The spines of various species of cactus and those of the barberry (*Berberis*) (Fig. 163) are formed by the transformation of the whole leaf. In the black locust (*Robinia pseudacacia*) (Fig. 164) and in various species of *Euphorbia* there are paired spines at the base of the leaves. These are, no doubt, transformed stipules.

FIG. 163.—Leaf spines of common barberry (*Berberis vulgaris*). A short shoot bearing ordinary foliage leaves stands in the axil of the branched spine-like leaf.

FIG. 164.—Stipular spines of black locust (*Robinia pseudacacia*).

Food Storage.—In the monocotyledons, particularly in the Liliaceae, such as *Tulipa* and *Allium* (the onion), there are special scale leaves, which serve for food storage (Fig. 105). These make up the bulk of the bulbs which are characteristic structures of these and related plants.

Water Storage.—Special water-storing leaves are borne by many plants which live in dry soil and in salt marshes where water absorption is difficult

on account of the high concentration of the soil water. Examples of plants bearing such water-storing leaves are stone crop (*Sedum*), sea fig (*Mesembryanthemum*), and Russian thistle (*Salsola*). These

FIG. 165.—Water storage leaves. (Left), *Cotyledon orbiculata;* (center and right), two species of *Mesembryanthemum.*

leaves are generally much thickened and are provided with a very efficient cuticle. They are largely made up of **water tissue.** This tissue consists of large, very turgid, and swollen parenchyma cells which

generally lack chloroplasts and have large central vacuoles. Large quantities of water, which the plant has absorbed over a considerable period or during a short season when water was abundant, are stored in these leaves so that it may be used as needed by the plant. When the leaves of such **succulent** plants are crushed they yield an astonishing quantity of water, but under natural conditions this water is held so tenaciously that some such plants can live, and even send out new shoots, when they have been severed for weeks or months from any connection with the soil.

Leaf Tendrils.—There are many plants whose leaves are wholly or in part transformed into tendrils by which the plant may attach itself to a support. Thus, in the sweet pea (*Lathyrus odoratus*), several of the uppermost pairs of leaflets of the compound leaf have no blades, but instead form slender cylindrical tendrils (Fig. 137). In *Lathyrus Aphaca* the whole leaf is transformed into a single tendril and the typical leaf functions are taken over by the leaf-like stipules. The petiole may serve as a tendril, as in the potato vine (*Solanum jasminoides*) and in the garden nasturtium (*Tropaeolum*); or that function may be performed by the stipules as in some species of *Smilax*, or by the rachis of the compound leaf, as in *Clematis*.

Capture of Insects by Leaves.—Without question, the most remarkable adaptation of leaves to a special function is found in the few plant species whose leaves are able, through various devices, to capture insects and secure food from their bodies. These **insectivorous** plants generally have weakly developed root systems, and are mostly found in locations where the essential minerals ordinarily secured from the soil are deficient in amount. Most of them are found in bogs where the soil is largely composed of decayed plant remains and is on that account, and because of the leaching effect of the abundant water which it contains, low in content of essential minerals.

The best-known insectivorous plants are the Venus' fly trap (*Dionœa muscipula*), sundew (*Drosera*), pitcher plants (*Nepenthes*, *Sarracenia*, and *Darlingtonia*), and bladderwort (*Utricularia*).

In Venus' fly trap, the two halves of the leaf blade each have a row of long stout teeth along the outer margin and three sensitive hairs in the center of the upper side. When an insect alights upon the leaf and touches one of these bristles the two halves fold together quickly along the midrib. The softer parts of the captured insect are rendered soluble by a digestive juice secreted by glandular hairs on the leaf surface.

In the sundews, the flat, more or less circular leaf blade is covered with long, radiating, glandular hairs covered at the tips with a sticky

FIG. 166.—Leaves of Venus' fly-trap (*Dionœa muscipula*). One leaf blade is shown fully open, several are partly open, and at left is one of the halves of which have closed, entrapping an insect. The sensitive hairs in the center of the lobes of the leaf blades do not show in this illustration. (Photograph by John Howard Payne from the *Journal of Heredity.*)

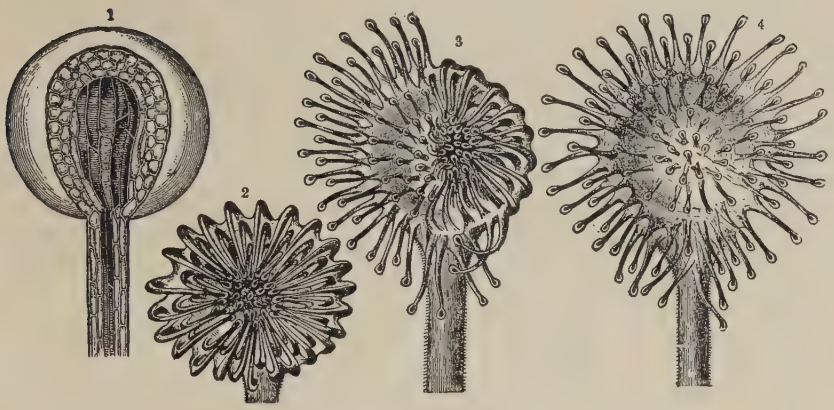


FIG. 167.—Sundew (*Drosera*). 1, Lengthwise section of a gland at the tip of a tentacle; 2, leaf with all tentacles incurved; 3, leaf with half of tentacles incurved over a captured insect; 4, leaf with all tentacles extended. (After Kerner.)

FIG. 168.—Pitchers of four insectivorous plants. *A*, *Sarracenia variolaris*. *B*, *Darlingtonia californica*. *C*, *Sarracenia laciniata*. *D*, *Nepenthes villosa*. (After Kerner.)

secretion containing a digestive enzyme. Insects alighting on these hairs are held fast and eventually digested by the secretion. The digested material from the insect is presumably absorbed by the plant.

In the pitcher plants, the entire leaf or a part of the leaf forms an urn or pitcher, which is partly filled with a liquid in which the captured insects drown and are subsequently digested.

The bladderwort (Fig. 169) is a rootless, submerged water plant, which bears numerous small bladders on the branches. Each of these

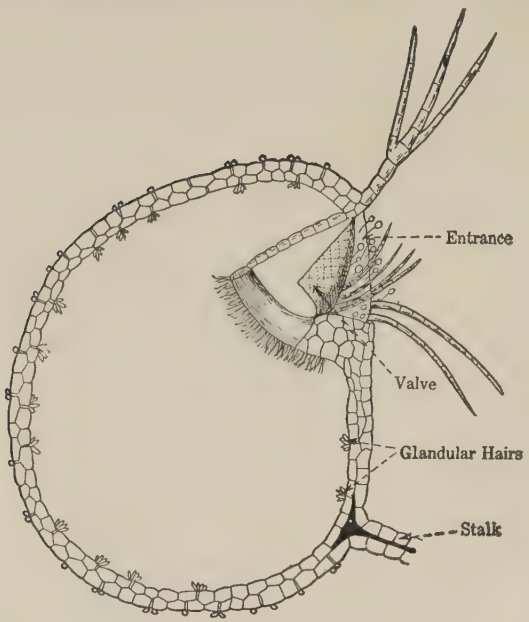


Fig. 169.

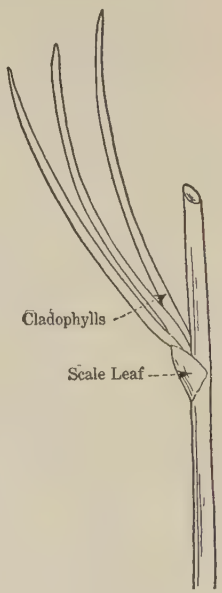


Fig. 170.

Fig. 169.—Insect trap of *Utricularia* in section. (Redrawn from Sachs.)

Fig. 170.—A portion of the stem of asparagus showing a scale leaf and the needle-like stems (cladophylls.)

bladders has a single opening to the exterior, closed by a sort of valve or trap-door, which opens only inward. Small water animals which enter these traps are therefore unable to escape.

Organs Other than Leaves which Perform the Typical Functions of Leaves.—In the tropical orchid (*Taeniophyllum*) and in one or two related genera, the plant body is without foliage leaves, and there is no stem, except a very short and temporary one, which supports the flower As a result, the leaf functions are performed by the roots.

These, instead of being covered with soil, are attached to the surface of a tree trunk and perform all the functions of the plant except that of reproduction. They are green in color and much flattened.

In the Scotch broom (*Spartium*) and in various species of *Euphorbia* which live in dry habitats, the true leaves are small and are shed soon after they are formed, in order, it would seem, to reduce the transpiring surface. Thus the functions typical of leaves, photosynthesis and transpiration, are taken over by the stems, which show, however, in these plants, little evidence of change in form to adapt them to these functions.

In other cases the stems which have taken over leaf functions have become adapted in form to these functions. Thus in asparagus (Fig. 170) the true leaves, which are small and scale-like, bear in their axils slender shoots which look much like leaves.

CHAPTER VII

THE FLOWER

Vegetative and Reproductive Functions.—Up to this point we have discussed the plant organs which are primarily concerned with the vegetative functions, i.e., with those functions through which the individual plant provides for its own needs. The function of reproduction has nothing to do with the welfare of the individual plant which carries on this function. In fact, in the case of many plants reproduction is always a forerunner of the death of the individual plant. The reproductive function serves to originate new individuals and thus to perpetuate the species, to multiply the number of plants of the species, and to distribute the species over a larger area. In this and the following chapters we shall discuss the plant structures (flower, fruit, and seed) which have to do directly with reproduction, and the processes (pollination, fertilization, seed development, and germination) by which reproduction is accomplished.

Some of the particulars of the reproductive processes among the higher plants will be taken up in more detail in the second part of this book, where it will also be shown how the organs and methods of reproduction among the Spermatophytes, or flowering plants, have evolved from those of more primitive plants.

What is a Flower?—A flower is really a stem, generally a branch stem, bearing leaves which are specially adapted to carry on reproduction. Such floral leaves are very different in form from foliage leaves. The flower has its origin in the axil of a leaf, just as does an ordinary branch. The leaf which thus **subtends** a flower is ordinarily quite unlike a foliage leaf and is called a **bract.** Though really a branch, the flower differs from branches bearing foliage leaves in the following three important particulars:

1. The primordial meristem of this branch does not continue to grow but is " used up " in formation of the floral leaves which make up the flower.

2. The floral leaves, instead of being distributed at intervals along the stem and being separated by long internodes, are crowded together.

3. Normally there are no buds in the axils of the floral leaves.

THE PARTS OF A TYPICAL FLOWER

Among the typical flowering plants there is a very large number of different flower forms. With relatively few exceptions, they are made up of the same parts, although they vary in the number, form, and arrangement of these parts. The parts which make up a typical flower are the following (Figs. 171 and 172).

The Essential Flower Parts:

Pistils, each consisting of

1. Ovary (basal part of the pistil which becomes the fruit).
2. Style (column of tissue arising from the top of the ovary and through which the pollen tube grows).
3. Stigma (expanded tip of style to which pollen adheres)

Stamens, each consisting of

1. Anther (the pollen-bearing body).
2. Filament (stalk or support to the anther).

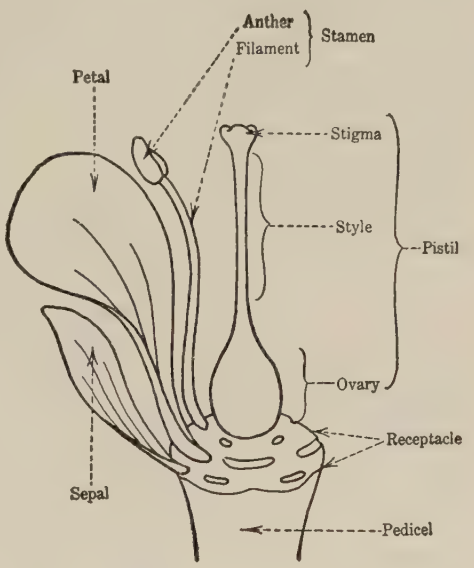


FIG. 171.—Diagram of a flower from which all but one of each whorl of flower parts have been removed. (Modified after Hall from *A Yosemite Flora*.)

The Accessory Flower Parts:

Petals (collectively called the *corolla*).

Sepals (collectively called the *calyx*).

Peduncle.

Receptacle.

The petals and sepals taken together are called the **perianth.**

If a flower is borne singly its stalk or stem is called a **peduncle.** In many plants, however, the flowers are borne in clusters or **inflorescences.** In the latter case the stems (generally short) which bear the individual flowers of the cluster are called **pedicels;** and the main stem of the cluster or inflorescence, from which the pedicels arise, is called the peduncle of the inflorescence. In short, a **peduncle** is the stem or stalk of a solitary flower or of an inflorescence, whereas the stalk of each

flower of the cluster is a **pedicel.** The end of a peduncle or of a pedicel is generally broadened out to form a structure called the **receptacle,** to which the floral parts proper are attached.

In a typical flower the center is occupied by the pistil or pistils; in a circle of whorl surrounding these are the stamens; outside the stamens is a circle of petals; and surrounding these a whorl of sepals.

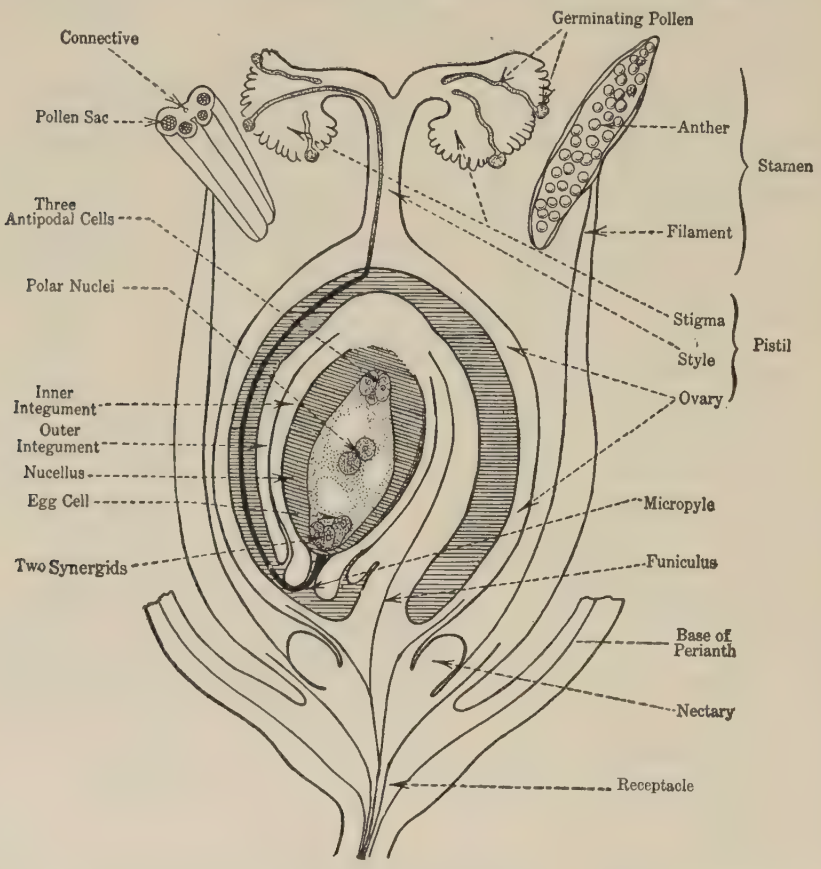


FIG. 172.—Diagrammatic lengthwise section of a flower. (Redrawn from Sachs.)

The pistils and stamens are spoken of as the essential flower parts, because if either stamens or pistils are lacking there can be no seed formation by the flower, and reproduction, the sole function of the flower, can not be accomplished. The petals and sepals, though not essential for seed formation, are important in protecting the stamens and pistils before the flower bud has opened and in attracting the insects,

which in most flowers, as we shall see later, are needed to bring about seed production.

ORIGIN AND DEVELOPMENT OF THE FLOWER PARTS

In plants which bear their flowers in inflorescences, a single such cluster may contain flowers in various stages of development. The flowers at the base of such a group may be fully developed or may even have produced fruits, while at the extreme tip of the inflorescence there may be flower buds of microscopic size in which the flower parts are mere rudiments. The sepals, petals, stamens, and carpels (floral leaves which, single or fused into groups, form the pistils) make their first appearance as protuberances of meristematic tissue from the growing point of the end of the floral branch (Fig. 173). These protuberances or **primordia of flower parts** thus arise in a manner similar to the primorida of foliage leaves. There are, however, two important points of difference: (1) In the leaf bud the growing point or primordial meristem of the shoot can continue indefinitely to produce leaf primordia. These primordia are always produced on the sides of a growing point which continues to elongate at the tip. The growing point of a developing flower, however, does not continue to grow after the rudiments of flower parts have been formed, for the very tip of the growing point is involved in the formation of the carpels. It is interesting to know that in certain abnormal flowers or flower monstrosities not all of the growing point is used up in the formation of the flower, and the stem grows on through the flower and gives rise to foliage leaves.

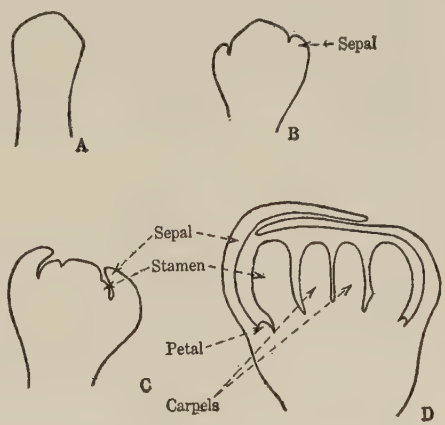


Fig. 173.—Origin and development of flower parts of shepherd's purse (*Capsella*). *A*, apex of the floral axis before the appearance of the primordia of any of the flower parts. *B*, appearance of sepals. *C*, the stamens have made their appearance and the carpels are just beginning to form. *D*, the petals have appeared and the primoridia of the carpels also. Note that the latter in their formation involve all that remains of the promeristem of the floral axis. (Redrawn from Coulter and Chamberlain.)

(2) In the development of leaf primordia those nearest the end of the

growing point are always the smallest and are the ones most recently formed, while in the formation of the flower parts there may not be such an orderly development. For example, in the common shepherd's purse (*Capsella*), the rudiments of the sepals, stamens, and carpels attain considerable size before the rudimentary petals appear.

For some time after they appear, the small projections of meristematic tissue, which are to become flower parts, elongate by cell division and cell growth. Later, in many flowers, a ring or zone of tissue at the base of one or more whorls of primordia begins to grow actively so that the primordia are carried up on a circular ridge of tissue common to all the parts of a whorl or in some cases to several whorls. This development may result in the separate parts of any one whorl being more or less united with each other in the mature flower, a condition called **coalescence.** In other cases two or more whorls may become grown together to a greater or lesser extent, a condition called **adnation.** Since coalescence and adnation are responsible for various characteristic types of flower formation, we shall have occasion to refer to them later.

HISTOLOGY OF THE FLOWER PARTS

Whereas the peduncle (or pedicel), the receptacle, and the ovary are relatively long-lived structures, the stamens, petals, and sepals are normally very short-lived. Partly on account of their short life, and partly because they do not perform such vegetative functions as conduction of water to other parts, food manufacture, and food storage, the stamens, petals, and sepals are much simpler in their internal structure than are the vegetative organs of the plant.

The peduncle (or pedicel) has much the same structure as have stems which bear foliage leaves. In some plants the sepals are very leaflike both in external appearance and in their anatomy. In other cases they are very similar to the petals and like them are largely made up of parenchyma cells, and have a finely branched system of very small vascular bundles, and an epidermis with practically no cuticle and few, if any, stomata. Except for the cells which develop into pollen grains, the stamens are as simple in their histology as the petals, for they consist of thin-walled parenchyma cells, one very much reduced vascular bundle, and an epidermis having little or no cuticle. The same may be said of the pistil, although the fruit into which the ovary develops generally has a well-developed epidermis, sometimes with exceedingly thick cuticle. The fruit may also possess considerable mechanical tissue, such as the stone cells (sclerenchyma) in the flesh of pear fruits and in the stony layer or " pit " of the peach, cherry, and plum. Con-

ducting tissue is also well developed in some fruits. Chloroplasts are very generally present in the cells of the pistil and the sepals.

Sepals.—In the flower bud the petals, stamens, and pistils are usually enclosed within the calyx. This protects the parts within from mechanical injury, from rain, and from drying out. In keeping with the protective function which they serve in the bud, the sepals are generally of firmer texture than the other flower parts. Sometimes when the petals are lacking, as in *Clematis*, the sepals, instead of being relatively small, green and leaf-like, become large, delicate, and highly colored structures very similar to typical petals, and perform the same function as the petals.

Petals.—In typical flowers the petals attract insects, which may carry pollen from the stamens of one flower to the tip of the pistil (stigma) of another. This transfer of pollen from the stamen to the stigma is essential to seed formation. The petals may attract insect visitors not merely by their large size and conspicuous coloration but also by the perfume which they frequently produce, and in many cases by the sweet product (nectar) of sugar-secreting glands or **nectaries.**

The color of the petals may be due (1) to pigments dissolved in the sap of their cells or (2) to pigments contained in chromoplasts. Often both methods of coloration are combined. The colored substances dissolved in the cell sap of the vacuoles are generally anthocyanin pigments, and the resulting coloration is red, blue, or violet, as in the garden geranium (*Pelargonium*), *Iris* and violet (*Viola*). The color of these pigments changes with the acidity of the cell sap. The change in shade of many red or blue flowers as they grow older is due to a progressive change in acidity within the cells. Carotin is principally responsible for the yellow, orange, and red colorations of petals in which the pigment is in the chromoplasts. Some of the colors of wallflowers (*Cheiranthes*) and of nasturtium (*Tropaeolum*) (in this case, of the sepals) are due to the presence in certain of the cells of both colored sap and chromoplasts. In the case of white petals no pigments are present. The intense whiteness is due to the reflection of light from the numerous air-filled intercellular spaces in the tissue, just as foam is white because of the reflection of light from air masses within the bubbles. If the intercellular spaces are filled with water or alcohol the petals are no longer white.

The odor produced by the petals is due to ethereal oil and esters excreted by certain special cells. Odor and color are in many cases both used by the same plant to attract insects. Very showy flowers, however, are often without odor, and inconspicuous flowers, if insect-pollinated, are generally fragrant.

The nectaries, commonly found near the base of the petals but fre-

quently located elsewhere in the flower, are glands which secrete water and sugar.

Stamens.—It was stated earlier in this chapter that the various flower parts are really leaves which have been adapted to perform certain functions in reproduction. The expanded form of the sepals and petals, the leaf-like appearance of the sepals of many flowers, and the fact that the sepals of some flowers are petal-like make it relatively easy to accept the statement that the sepals and petals are really leaves. The stamens, however, certainly do not generally resemble foliage leaves in any way. Nevertheless, a study of the evolution of the flowering plants indicates that the stamens are in all probability structures evolved from the special spore-bearing leaves (sporophylls) of lower plants. The stamen stalk or filament corresponds more or less closely to the petiole of a leaf, and the anther may be considered to be a much reduced leaf blade bearing four pollen sacs. The filament serves merely to support the anther, while the latter performs the essential function of the stamen, which is pollen production. The anther consists of two lobes, running lengthwise, and united by a band of tissue called the connective. If an unripe anther is cut crosswise it can be seen that each lobe contains two longitudinal cavities, **pollen sacs,** within which the pollen grains are produced. When the pollen is ready to be shed, these open, generally by longitudinal slits. The form of the stamens is remarkably uniform in most flowers, but there are numerous peculiar departures from the common type.

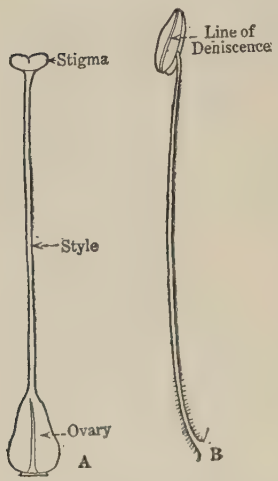


FIG. 174.—The essential flower parts of tobacco (*Nicotiana*). *A*, the compound carpel consisting of two carpels. *B*, a stamen, showing the filament (stalk) and anther.

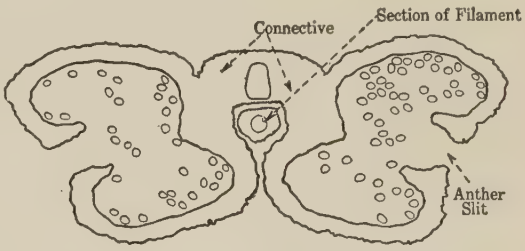


FIG. 175.—Cross section of an open anther of lily (*Lilium*). Note that the walls separating the two pollen sacs of each anther lobe (*theca*) have broken down so that but one chamber now exists in each half of the anther.

Pistils.—These flower parts are also made up of modified leaves.

If a pistil shows evidence of consisting of a single such leaf (carpel) it is spoken of as a simple pistil. The flowers of the buttercup (*Ranunculus*) and of the strawberry (*Fragaria*) have **simple pistils.** When, as is more commonly the case, a number of carpels together form a single pistil, it is called a **compound pistil.** Examples of plants with compound pistils are tobacco (*Nicotiana*) with two carpels, lilies (*Lilium*) with three, and poppy (*Papaver*) with many carpels. Whether the pistil be simple or compound it almost always has three parts: (1) an enlarged basal part called the **ovary,** which is just above the attachment to the

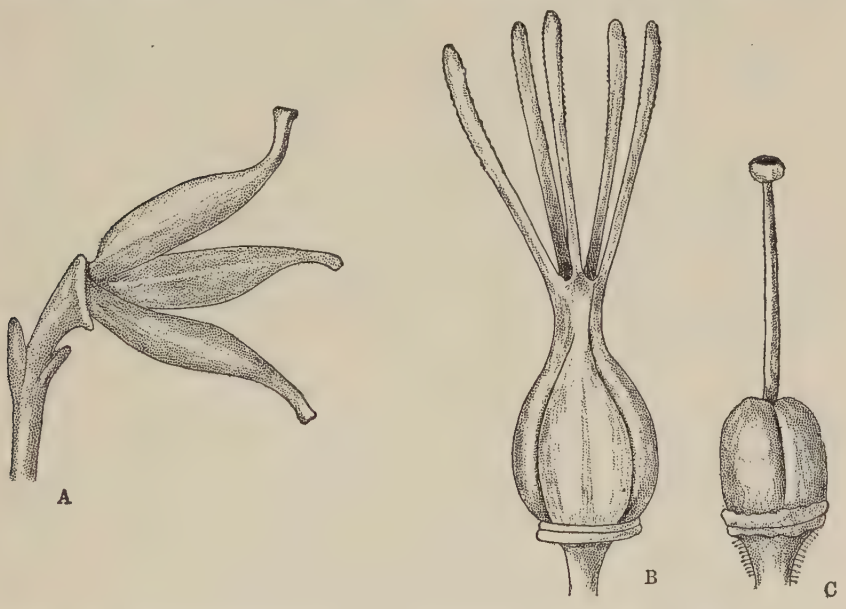


FIG. 176.—Three types of pistils. *A*, apocarpous. *B*, compound with styles free. *C*, compound with one style. (Redrawn from Berg and Schmidt.)

receptacle, and which becomes the fruit; (2) a column of tissue arising from the top of the ovary and called the **style;** and (3) a more or less expanded part at the upper end of the style, called the **stigma.** The stigma generally has its surface roughened by short, cellular protuberances. It sometimes secretes a sweet and sticky solution, the **stigmatic fluid.** In wind-pollinated plants (e.g., grasses), the stigma is often much branched. The style may be very short or even lacking. In Indian corn (*Zea mays*), the styles (corn silk) are very long and filamentous.

As already stated, the pistil is made up of one or several foliar structures called **carpels.** It seems likely that in the plants, now

extinct, from which the flowering plants (angiosperms) were evolved, the carpels were much more leaf-like than they are in the flowering plants of our time and that they bore the rudimentary seeds or **ovules** attached to their margins. In the evolution of the angiosperms there probably came about a fusion of the edges of each carpel or of several carpels so that the ovules came to be borne within a chamber. At the same time the apex of the carpel or of several united carpels was elongated to form the style and the stigma. In the case of flowers with simple pistils (each consisting of but one carpel) the ovary has a single cavity (**locule**). In such a pistil the line of union of the two edges of the carpel is called the **ventral suture** and the line corresponding to the midrib of the leaf (carpel) is called the **dorsal suture.** When the simple pistil of the bean and of most other members of the pea or legume family (*Leguminosae*) develops into a fruit (pod) it splits easily along these two sutures.

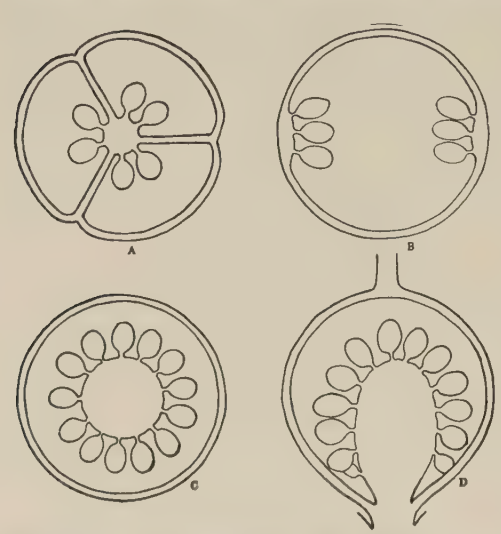


FIG. 177.—Diagrams showing the three principal types of placentation. *A*, axile. *B*, parietal. *C*, free central, cross section of ovary. *D*, free central, lengthwise section of ovary.

In compound pistils the number of locules commonly corresponds to the number of carpels. The carpels of a compound pistil may, however, fuse with each other along their edges so that a single chamber or locule is enclosed. In some cases the ovary of a simple pistil may be divided into several locules.

The regions within the ovary to which the ovules are attached are called **placentae** (singular **placenta**) (Fig. 177); and the mode of attachment is called placentation. In most flowers the number of placentae is the same as the number of carpels in the pistil and in such cases the placentae generally correspond quite evidently to the in-rolled and united edges of the carpels. If the placentae are on the ovary wall, as in the currant and gooseberry (*Ribes*) (Fig. 177, *B*) they are said to be **parietal.** If they are borne on the axis of an ovary which has several locules, as in lilies (*Lilium*), they are said to be axile (Fig. 177, *A*). Of

much less frequent occurrence than parietal or axile placentation is **central** placentation, in which the ovules are borne on the axis of a unilocular ovary (ovary with but one locule). This type of placentation occurs in the primrose family (*Primulaceae*) (Fig. 177, *C*, *D*).

The number of ovules in an ovary ranges from one, as in the buckwheat family (*Polygonaceae*) and the grass family (*Gramineae*), to many hundreds in tobacco (*Nicotiana*) and most orchids. The ovules are small structures, generally oval in form and attached to the pla-

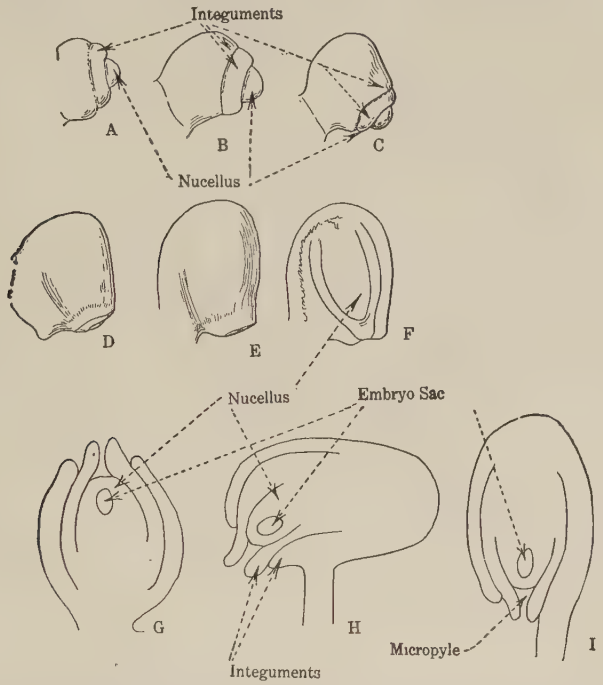


FIG. 178.—*A–F* stages in the development of an anatropous ovule; *G*, atropous ovule; *H*, campylotropous ovule; *I*, anatropous ovule. (*F* to *I*, in section.) (*A–F*, redrawn from Gray; *G–I*, redrawn from Prantl in Engler and Prantl's Nat. Pflanzenfam.)

centa by a short stalk called the **funiculus.** In most plants the **funiculus** is sharply bent at the base of the ovule so that the ovule tip is directed downward toward the placenta. Such ovules are called **anatropous ovules.** Ovules in which the axis of the ovule is continuous with that of the funiculus are called **atropous ovules.** They occur in the knotweeds (*Polygonum*) and many other plants. A third type of ovule, more or less intermediate between the two preceding types, is the **campylotropous ovule.** In this type the ovule is bent. It is found in

many members of the pink family (*Caryophyllaceae*). Figure 178, *G-I* represents these three types diagrammatically.

Figure 179 shows a series of stages in the development of an ovule. The ovule first appears as a slight protuberance upon the surface of the placenta. This protuberance develops into a projecting mass of tissue with rounded end (the **nucellus**). From the base of this there arise later two rings of tissue which grow up around the nucellus and enclose it except for a narrow pore at the end of the ovule. The two layers of tissue which thus surround the mature ovule are called the **inner integument** and the **outer integument.** The pore leading from the outer surface of the ovule between the edges of the two integuments down to the surface of the nucellus is called the **micropyle.** Buried in the tissue of the nucellus in a mature and fully developed ovule is the **embryo sac** which is of great importance in the process of sexual reproduction by which the ovules become transformed into seeds. Figures 172 and 180 show fully developed ovules in longitudinal section. In these it can be seen that the embryo sac consists of a mass of vacuolated cytoplasm with eight nuclei lying free in it. The two nuclei lying nearest to the micropylar end of the embryo sac are the so-called **synergids;** near them is the **egg nucleus.** At the opposite extremity of the embryo sac are also three nuclei termed the **antipodal nuclei.** In many plants each of these nuclei, together with a little cytoplasm, becomes surrounded by a cell wall so that they can in such cases be best spoken of as antipodal cells. Between the egg apparatus (egg nucleus and synergids) and the antipodal nuclei there are two nuclei which lie near each other or in actual contact. These are the **polar nuclei.** In our discussion of seed formation we shall recur again to the structure of the embryo sac and shall state the part played by the various nuclei of the embryo sac in that process.

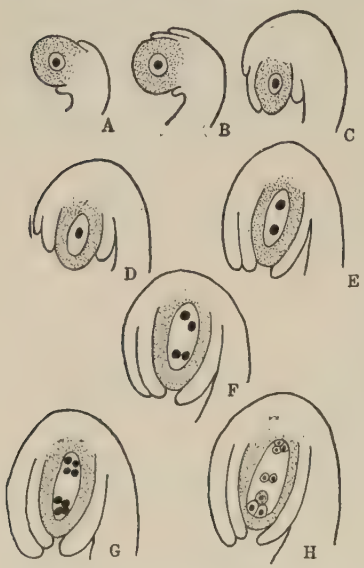


FIG. 179.—Stages in the development of the ovule of *Lilium* (lily). *A*, inner integuments beginning to grow up about the nucellus. *B*, outer integuments are appearing. The continued growth of these integuments is shown in the figures which follow (*C–H*). (Redrawn from Gager.)

TYPES OF FLOWERS

Thus far we have described the features common to all or most flowers but actually flowers are very diverse in size, color, structure, and many other respects. We shall attempt to point out only a few of the most conspicuous and most important of the differences of flower structure commonly met with.

1. **Absence of Certain Parts.**—The flower described on page 235 was **complete,** that is, all of the usual flower parts (sepals, petals, stamens

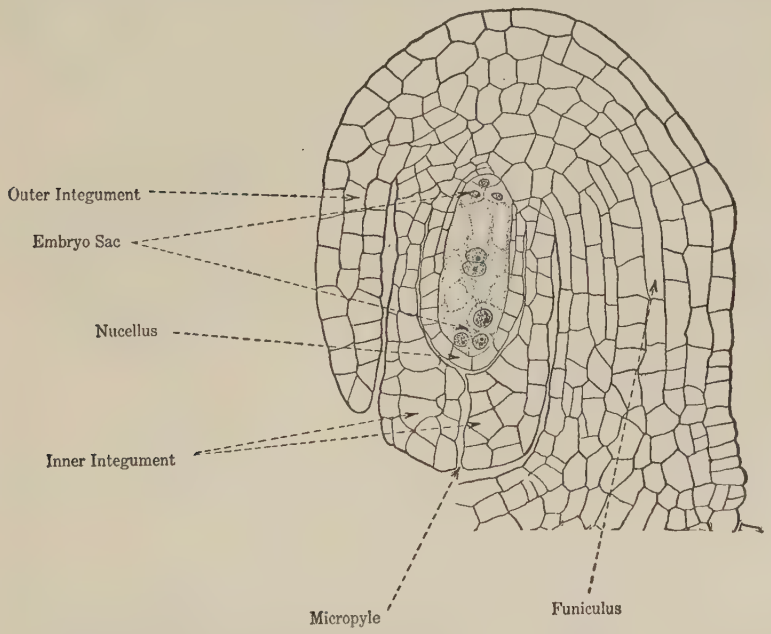


FIG. 180.—Longitudinal section of a lily (*Lilium*) ovule showing the embryo sac ready for fertilization. At the end of the embryo sac nearest to the micropyle are the two synergids and the egg cell; at the opposite end are the antipodal cells and in the center are the polar nuclei.

and carpels) were present. A great many species of plants have flowers which are lacking in one or more of the four kinds of flower parts present in typical flowers. In many such **incomplete** flowers the perianth (sepals and petals) is absent, in other cases the calyx is present but the corolla is lacking, and in still other incomplete flowers it is one or the other of the essential flower parts (stamens or carpels) which are not present.

Flowers without Perianth.—The absence of the perianth or its reduction to mere scales or hairs is characteristic of the flowers of such monocotyledons as the grains and grasses (*Gramineae*) (Fig. 182), the sedges (*Cyperaceae*), the calla lily family (*Araceae*), and, among the dicotyledons, of the willow family (*Salicaceae*) which includes the willows and poplars, of the alder (*Alnus*), the sycamore (*Platanus*), and many other plants. With very few exceptions, flowers that have no perianth are wind-pollinated and have no need for conspicuous flower parts to attract insects. It is an interesting fact that most plants whose flowers lack a perianth and are wind-pollinated have evolved from plants which were insect-pollinated and whose flowers possessed a perianth.

Flowers Having Calyx but Lacking Corolla.—Many of the flowers which have sepals but lack petals are inconspicuous and apparently not

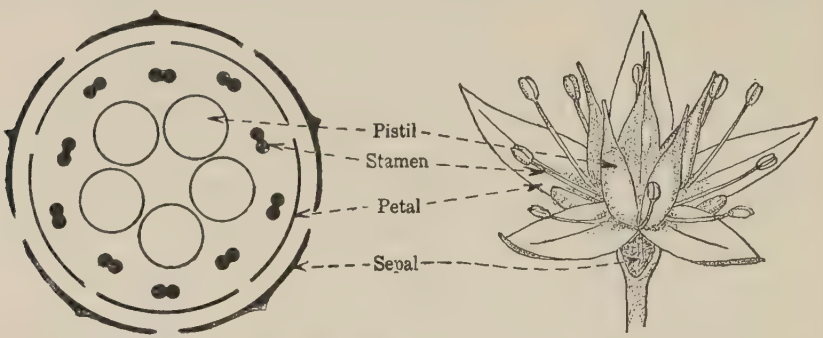


FIG. 181.—A flower of *Sedum acre* (a stonecrop). To the left of the drawing of the flower is a floral diagram showing the number and arrangement of the flower parts.

fitted to attract insects; but in other cases the sepals are large and conspicuously colored or formed, and so take the place of the petals in relation to insect pollination. The Nettle family (*Urticaceae*) and the Goosefoot family (*Chenopodiaceae*), to which belong the beet (Fig. 183) and the pigweed, furnish examples of plants with apetalous flowers without conspicuously petal-like sepals. *Clematis*, wild ginger (*Asarum*) and Dutchman's pipe (*Aristolochia*) are plants whose flowers lack petals but whose sepals serve the usual function of petals.

Flowers Lacking One of the Essential Parts.—Some plant species bear no flowers that have both stamens and carpels. It is clear that in such cases there must be two kinds of incomplete flowers if seed production is to be accomplished, namely, stamen-bearing or **staminate** flowers and pistil-bearing or **pistillate** flowers. Such flowers are said to be **diclinous** or **imperfect** to distinguish them from the **hermaphrodite**

FIG. 182.—Common oats (*Avena sativa*). (Right)—the inflorescence, a panicle. (Upper left)—a single spikelet; *b*, pedicel; *c*, lower empty glume; *d*, upper empty glume; *e*, lemma with dorsal awn (*f*); *g*, sterile flower. (Lower left)—a single flower; *h*, rachilla; *i*, palet; *j*, lodicules; *k*, anther; *l*, ovary; *m*, plumose stigma. (After Jepson, from *Flora of Economic Plants*.)

or **perfect** flowers (flowers with both stamens and carpels) borne by most plants. Diclinous species in most cases have been evolved by reduction from ancestors which had perfect flowers.

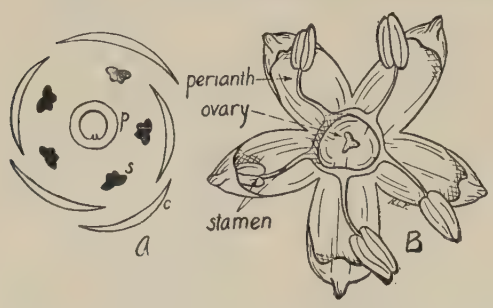


FIG. 183.—Flower of beet (*Beta vulgaris*), which has a calyx but lacks a corolla. *A*, floral diagram. *B*, face view. (After Robbins, from *Botany of Crop Plants*.)

In some cases both staminate and pistillate flowers occur upon each individual plant of the species. Such plants are said to be **monoecious**. This is the case in Indian corn or maize (*Zea mays*) where the tassel is a group of staminate flowers and the young ear a group of pistillate flowers. Other familiar examples of monoecious plants are the hazel (*Corylus*), oak

FIG. 184.—The imperfect flowers of field pumpkin (*Cucurbita pepo*). *A*, staminate flower. *B*, pistillate flower. (After Robbins, from *Botany of Crop Plants*.)

(*Quercus*), cucumber (*Cucumis*), and walnuts (*Juglans*). When the pistillate flowers are produced by one individual plant and the staminate by another, the species is spoken of as **dioecious.** In such cases there will be no seed production unless at least two individuals (a staminate plant and a pistillate plant) are growing near enough together for the pollen to be transferred. There are relatively few dioecious species. Some of the most familiar are the date palm (*Phoenix dactylifera*), the hop (*Humulus*), asparagus, the willows (*Salix*), and cottonwood and other poplars (*Populus*). In certain cultivated dioecious species one of the two kinds of plants is much more desirable from the grower's standpoint than the other. Thus, staminate cottonwoods are preferred to pistillate ones because of the litter produced by the "cotton" covered seeds; in the date palm and the tropical papaya tree (*Carica*) it is desirable that most of the individuals be pistillate, since these alone can bear the edible fruit. There are many cases where a species bears, in addition to pistillate and staminate flowers, perfect (hermaphrodite) flowers also. Such species are said to be **polygamous.** Examples of such plants are certain maples (*Acer*), and some species of ash (*Fraxinus*).

FIG. 185.—The imperfect flowers of field pumpkin (*Cucurbita pepo*) with perianth removed. *A*, pistillate flower. *B*, staminate flower. (After Robbins, from *Botany of Crop Plants.*)

2. **Spiral Arrangement of Flower Parts.**—Although by far the greater number of flowers are **cyclic,** that is, have the flower parts disposed in circles or whorls about the axis of the flower, there are plants in which the arrangement of one or more sets of flower parts is spiral. When they are so arranged the number of the parts is generally greater than in flowers with cyclic arrangement.

3. **Differences in the Number of Parts in Different Whorls.**—In many flowers the number of members in each of the whorls is the same. Such flowers are said to be **isocyclic.** Examples of isocyclic flowers are the flag (*Iris*), some species of *Rhododendron* and certain species of

Crassula. In most flowering plants the stamens are more numerous than any of the other flower parts and frequently the number of carpels is less than that of any other members. Thus in the turnip (*Brassica campestris*) and all the other plants of the mustard family (*Cruciferae*) there are four sepals and four petals but six stamens and only two carpels; and in the pea and in all the other familiar members of the bean family (*Leguminosae*), though the sepals and petals are each five in number, the stamens are ten and there is but a single carpel (Fig. 186). The flowers of the great majority of plants are **heterocyclic** like those just mentioned.

4. **Differences in Form Among the Members of a Whorl.**—The majority of flowers are typically star-shaped, that is, have a corolla made up of similarly shaped petals equally spaced and radiating out from the center of the flower (Fig. 181). Flowers of this type almost always have a similar arrangement of the other flower parts and are usually **regular** flowers in that all the members of each whorl are of the same form. Such flowers are spoken of as **actinomorphic** (star-shaped). An actinomorphic flower may be defined as one that may be cut by at least two different planes into two halves, one of which is like the mirrored image of the other. Such a condition in a flower or any other structure is often spoken of as **radial symmetry.** This condition is so common that it will not be necessary to cite examples.

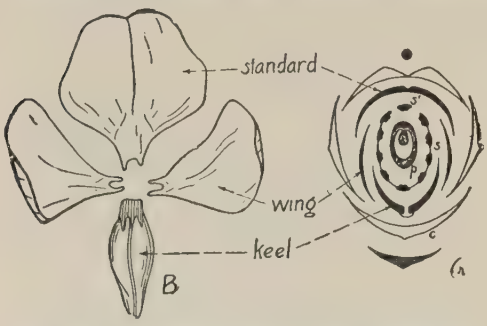


FIG. 186.—Bilaterally symmetrical, syncarpous flower of a legume (*Leguminosae*). *A*, floral diagram of horse bean (*Vicia faba*). *B*, corolla of a sweet pea flower (*Lathyrus odoratus*), dissected, diagrammatic. (*A*, after Eichler, *B*, after Bergen, from Robbins' *Botany of Crop Plants.*)

There are, however, many flowers which are not "star-shaped" and generally in these one or more members of at least one whorl are of different form from the other members of the same whorl. Among the most familiar examples of such **irregular** flowers are the blossoms of peas and beans and most other plants of the Leguminosae (Fig. 186) and of violet. In the peas and beans one petal (the **banner**) is broad and conspicuous. On either side of this are two somewhat narrower petals (the **wings**), and opposite the banner two smaller petals which are loosely united along their edges to form the **keel** which

encloses the stamens and pistil. In the violets the petals are not alike and one of them forms a tube or spur at its base; two of the stamens also are different from the other three and have spur-like appendages which bear nectaries. Flowers such as these do not have radial symmetry but at the most **bilateral symmetry,** which is to say that there is only one plane along which they can be cut into halves, each of which is like the mirrored image of the other.

5. **Flower Parts not Alternating.**—In the majority of flowers the petals alternate with the sepals and the stamens alternate with the

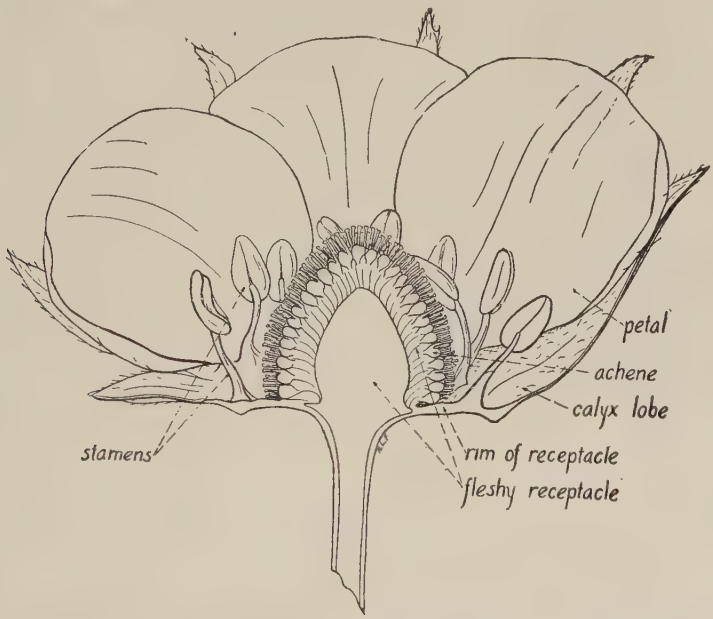


Fig. 187.—Median lengthwise section of the flower of strawberry (*Fragaria*) showing the numerous separate carpels attached to a common receptacle. (After Robbins, from *Botany of Crop Plants.*)

petals. In some cases, however, the parts of one whorl are opposite those of the next whorl. This is the case, for instance, in the pimpernel (*Anagallis*), shooting star (*Dodecatheon*), and other members of the Primrose family (*Primulaceae*).

6. **Union of Flower Parts.**—In most flowers, instead of all the parts being merely attached at the base to the receptacle and entirely free from each other, those of one or more whorls are to some extent united with each other or to the members of other whorls. Union of the parts of a whorl may involve carpels (**syncarpy**), stamens (**synandry**), petals (**sympetaly**) or sepals (**synsepaly**)

Syncarpy.—There are many plants whose flowers have but a single carpel, for example, all the pea or legume family (*Leguminosae*) (Fig. 186) and the barberry and most of its family (*Berberidaceae*). Most flowers which possess several carpels have the carpels more or less united. In some instances, however, as in strawberry (*Fragaria*) (Fig. 187) and raspberry and blackberry (*Rubus*), the flowers have numerous carpels which are not united. In mustard (*Brassica*), lily (*Lilium*), and azalea (*Rhododendron*) there are respectively two, three, and five carpels united to form a single pistil. Sometimes the fusion between carpels does not extend throughout their length, so that though there may be but one ovary there are several stigmas or several styles and stigmas as in flax (*Linum*) and wood sorrel (*Oxalis*).

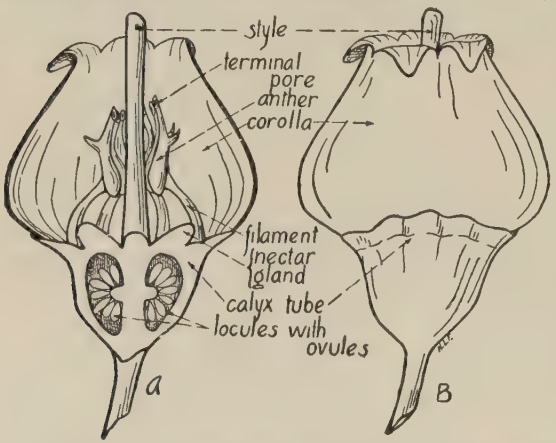


FIG. 188.—The epigynous flower of the huckleberry (*Vaccinium*), showing united sepals (*synsepaly*), united petals (*sympetaly*), and united carpels (*syncarpy*). *A*, median lengthwise section, *B*, external view. (After Robbins, from *Botany of Crop Plants.*

Synandry.—In the flowers of beans and peas and many related plants, nine of the ten stamens, or in some cases all ten, have their filaments united into a sheath which surrounds the pistil, but the anthers are free. In the Sunflower family (*Compositae*), on the other hand, the anthers are united and form a tube around the pistil while the filaments are free. There are many other flowers in which there is a union of the stamens.

Sympetaly and Synsepaly.—In many flowers the members of one or both perianth whorls are united along the edges with other members of the same whorl. There are many familiar flowers which show distinctly a more or less complete union of the petals. Morning glory (*Ipomœa*), azalea (*Rhododendron*), huckleberry (*Vaccinium*) (Fig. 188), potato (*Solanum*) (Fig. 190), tobacco (*Nicotiana*), and sunflower (*Helianthus*) are a few among many thousands of such sympetalous flowers. The plants bearing such flowers constitute together one of the three major divisions (**sympetalae**) into which the dicotyledons are sometimes artificially divided. As the corolla is often sympetalous, so the calyx is often synsepalous. Examples of partial or complete union of the sepals

along their edges are found in the flowers of sage (*Salvia*) and other mints (*Labiatae*), of evening primrose (*Oenothera*), of the pea or legume family (*Leguminosae*), and of several other families.

Union between Members of Different Whorls.—Union of the stamens with the carpels occurs very rarely. (The so-called column of the orchids is a structure resulting from the fusion of stamens and style, and in the Dutchman's pipe (*Aristolochia*) the same parts are united.) In many plants, as in pimpernel (*Anagallis*) and other members of the primrose family, in the morning glory (*Ipomœa*) and related plants, and in peppermint (*Mentha*), catnip (*Nepeta*) and all other members of the mint family, in potato (*Solanum*) (Fig. 189), tomato (*Lycopersicum*), pepper (*Capsicum*), and other members of the potato family (*Solanaceae*) the stamens are united at their bases to the petals. Such union of stamens and petals is spoken of as **epipetaly.**

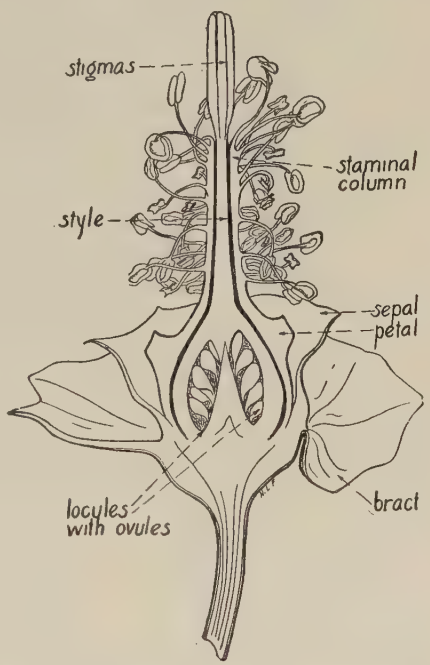


FIG. 189.—Flower of cotton (*Gossypium*) in median longitudinal section. In this, the filaments of the stamens are united (*synandry*) to form a long tube ("staminal column") enclosing the style. (After Robbins, from *Botany of Crop Plants.*)

Hypogyny, Perigyny, and Epigyny.—(Fig. 191.) When the receptacle is convex or conical, the whorls of flower parts are situated one above another and in the following order, beginning with the lowest: sepals, petals, stamens, and carpels. Such a flower is said to be **hypogynous** (Fig. 191, *A*). When the receptacle spreads out into a more or less deeply concave structure, at the center of which the pistil is attached, and at the margins or around the summit of which the sepals, petals, and stamens have their origin, so that these parts seem to be attached around instead of below the ovary (as in *Prunus*), the flower is said to be **perigynous** (Fig. 192). The ovary of a perigynous or hypogynous flower is said to be **superior.** If the concave receptacle not only surrounds the ovary but is fused with it, the other flower parts appear to

arise from the top of the ovary and the flower is spoken of as **epigynous** (Fig. 194). The fruits formed by epigynous flowers often bear at the unattached end the withered remains of the sepals and the stamens, or

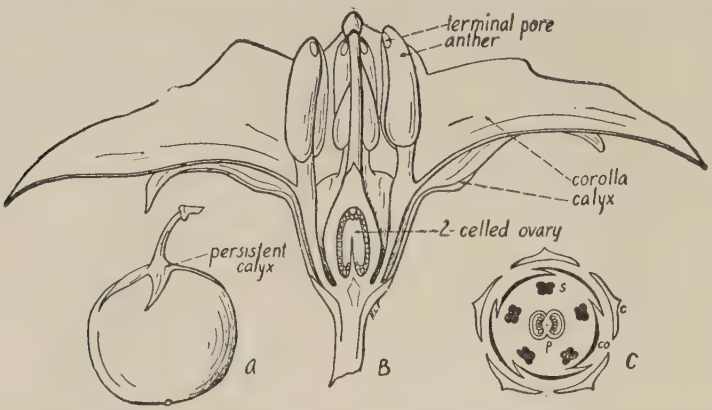


FIG. 190.—Flower and fruit of potato (*Solanum tuberosum*). *A*, mature fruit, a berry. *B*, median lengthwise section of the flower. *C*, floral diagram. Note that the stamens are attached to the sympetalous corolla. (After Robbins, from *Botany of Crop Plants*.)

of other flower parts. The raspberry (*Rubus*) and the strawberry (*Fragaria*) have hypogynous flowers; the cherry, peach, and plum (species of the genus *Prunus*) (Fig. 192) have perigynous flowers; and

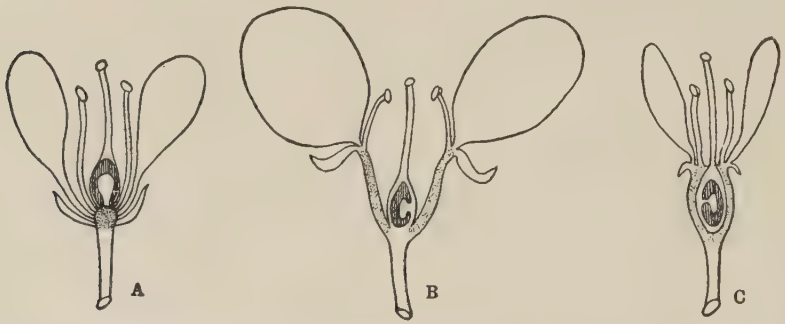


FIG. 191.—Diagrams showing the structure of hypogynous (*A*), perigynous (*B*) and epigynous (*C*) flowers.

the apple and pear (two species of the genus *Pyrus*) have epigynous flowers.

Two types of flowers deserve special discussion, both because they depart so far from the most typical in structure and because they are characteristic of two of the most important families of flowering plants—

the grass family (*Gramineae*), which includes all the grains, and the sunflower or aster family (*Compositae*).

The Structure of a Grass Flower.—In the grasses the flowers occur in small groups called **spikelets** (Figs. 182 and 193). A large number of these flower groups or spikelets are produced on one flower stalk and form an inflorescence. In some cases, as for example in wheat (*Triticum*), barley (*Hordeum*), and timothy (*Phleum pratense*), the spikelets are attached directly to an unbranched stem or **rachis** of the inflorescence

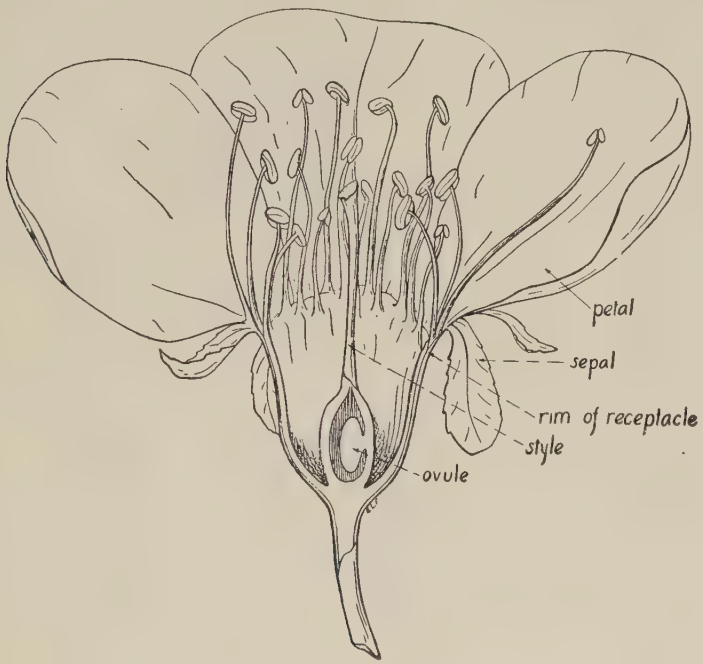


Fig. 192.—Perigynous flower of sour cherry (*Prunus cerasus*) in median lengthwise section. (After Robbins, from *Botany of Crop Plants.*)

which latter is then called a **spike.** In other cases the spikelets grow at the ends of branches of the rachis, forming an inflorescence which is known as a **panicle.** In the panicle of the oat (*Avena*) the branches of the rachis are long and slender.

The spikelet has a shortened axis, generally spoken of as the **rachilla** and this axis bears a number of chaffy, two-ranked, overlapping, bract-like structures. The two (rarely three or four) of these at the base of the spikelet are larger than the others and enclose the rest of the spikelet. They are called **glumes.** The number of flowers in a spikelet differs in different species. Each flower of the spikelet is enclosed between two

bracts which usually are very similar to the glumes but smaller in size. The lower of these bracts (the one with its back turned away from the rachilla) is the **lemma;** the upper one (with its back toward the rachilla) is the **palea** or **palet.**

The flower proper consists of a single pistil with three carpels (two abortive), three stamens, and two small scale-like structures (**lodicules**)

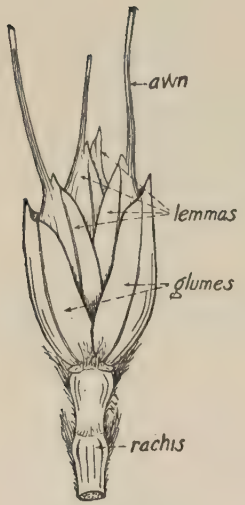


Fig. 193.

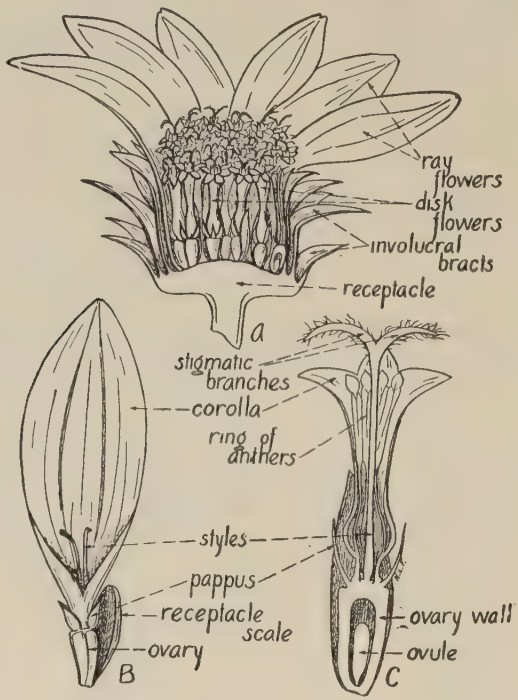


Fig. 194.

Fig. 193.—A single spikelet of wheat (*Triticum*). (After Robbins, from *Botany of Crop Plants.*)

Fig. 194.—Jerusalem artichoke (*Helianthus tuberosus*). *A*, longitudinal section of the head (*inflorescence*), showing the numerous separate flowers attached to a common receptacle. *B*, a single ray flower. *C*, a single disc flower, cut lengthwise. (After Robbins, from *Botany of Crop Plants.*)

which lie at the base of the ovary. The ovary contains a single ovule and has two feathery, much-branched stigmas. The stamens at maturity have very long and slender filaments and the anthers are **versatile,** that is, attached at about the middle to the end of the filament and in such a manner that they swing freely in the wind and are thus emptied of their fine, powdery pollen. The typical grass flower has no

sepals or petals but the lodicules probably represent two reduced perianth segments. The flower parts remain enclosed within the lemma and palea until they are mature and ready to function. Then if weather conditions are favorable the lodicules swell and force the lemma and palea apart so that the plume-like stigmas and the stamens protrude. At the same time the filaments rapidly elongate. Thus the anthers can readily discharge their pollen into the air and the stigmas may receive the wind-borne pollen.

The Structure of a Composite Flower.—In such plants as the sunflower (*Helianthus*), (Fig. 194) the aster (*Aster*), dandelion (*Taraxacum*), brown-eyed Susan (*Rudbeckia*), and the globe artichoke (*Cynara*), what we ordinarily speak of as a flower is, as a matter of fact, a compact inflorescence or group of flowers called a **head.** Each of these small flowers consists of (1) a pistil made up of two carpels and having an inferior ovary and a straight style with a two-parted stigma, (2) five stamens with filaments free but with anthers united into a tube which surrounds the style, (3) a corolla of five petals, and (4) a calyx which is reduced to a mere ring of tissue or to a cluster of scales or bristles, collectively called the **pappus.** In many of the *Compositae* there are two kinds of flowers in each head, **disc flowers** and **ray flowers.** The disc flowers make up the central part of the head, whereas the ray flowers are around the edge of the head. In the ray flowers, the corolla tube forms a strap-shaped (ligulate) structure which suggests a single petal of an ordinary flower. In some cases, as in the dandelion and lettuce (*Lactuca*), the heads are entirely made up of ligulate florets like those just described. In others, such as the globe artichoke (*Cynara*) and the burdock (*Lappa*), all the flowers are tubular as are the disc flowers. In those cases where there are both ray flowers and disc flowers the ray flowers are generally without stamens or may lack both pistil and stamens.

THE PRINCIPAL KINDS OF INFLORESCENCES

In many plants, such as *Anemone*, *Trillium*, and tulip (*Tulipa*), the flowers are borne singly at the end of a long flower stalk. In the great majority of flowering plants, however, the flowers are borne in groups or inflorescences resulting from the branching of the main axis or peduncle. There are many types of inflorescences depending (1) upon the manner of branching of the peduncle, (2) upon the time when different flowers in the group mature, and (3) upon the length of branches (pedicels) at the ends of which the flowers are borne. Almost all of these various inflorescences belong to one of two classes, (1) **indefinite** or **racemose** and (2) **definite** or **cymose.**

Racemose Inflorescences.—In racemose inflorescences the main axis continues to grow in length, as the result of the persistence of a primoridal meristem at the tip. New floral bracts (reduced leaves in

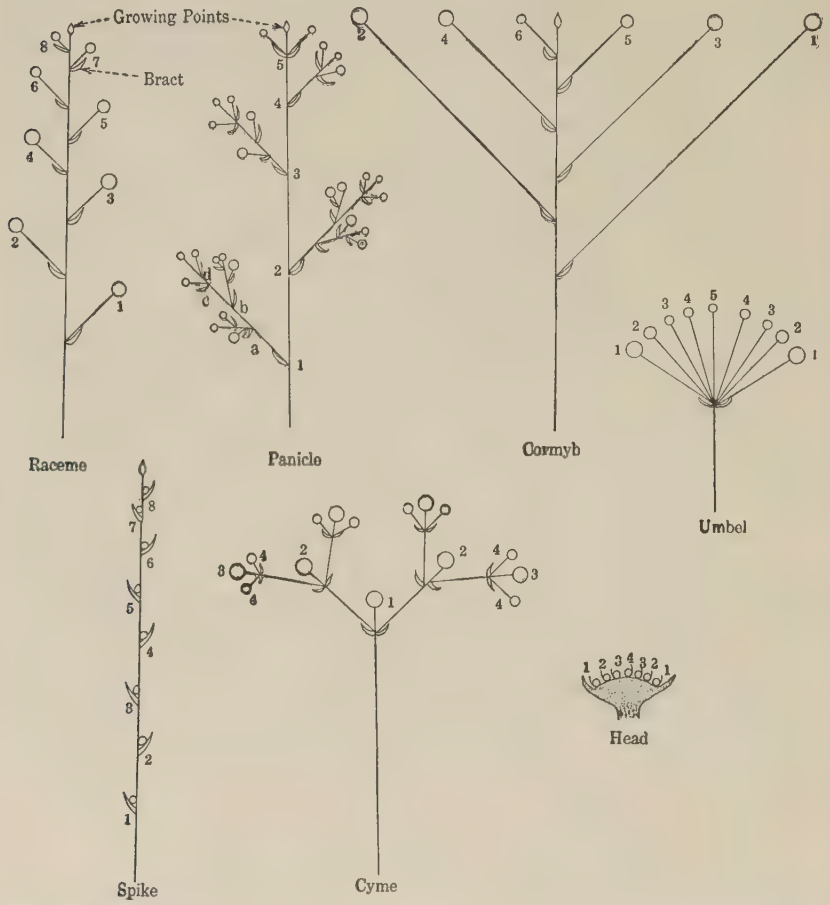


Fig. 195.—Diagrams showing the arrangement of flowers in some of the principal types of inflorescences. The flowers are represented by circles. Pedicels and subtending floral bracts are also shown. The numbers show the order in which the flowers of an inflorescence have developed, the flower marked 1 being in each case the oldest in the inflorescence. In the case of the panicle the letters *a–d* show the succession in which the flowers on the lowermost branch were formed. Note that all these inflorescences are racemose except the cyme.

the axils of which the flowers are borne) and new buds are formed at the growing point so that there is a more or less indefinite succession of flowers, the oldest being at the base of the inflorescence and the youngest

nearest to the growing point. In such flower clusters there may be flowers near the base of the inflorescence which have become mature and have given rise to fruits which are almost mature, while at the upper end minute buds containing very rudimentary flower parts may be forming.

Cymose Inflorescences.—In cymose inflorescences the apex of the main stalk ceases to grow very early, because the formation of a flower at the very tip involves the entire primordial meristem and thus prevents further elongation. The other flowers are produced on lateral branches further down the axis (rachis), and the youngest of the flowers in the cluster are found at the greatest distance from the tip of the peduncle. The principal characteristics of racemose inflorescences are given below in the form of a key.

KEY TO THE PRINCIPAL TYPES OF RACEMOSE INFLORESCENCES

I. **Simple Racemose Inflorescences.**—The flowers borne on the main axis of the inflorescence, either sessile or on pedicels.

1. The *Spike.*—The main axis of the inflorescence elongated and the flowers sessile. Example: The common plantains (*Plantago major*), and (*Plantago lanceolata*).

A. The *Catkin.*—A spike which generally bears only pistillate flowers or only staminate flowers and which eventually falls off from the plant entire. Examples: The willow (*Salix*) and the hazel (*Corylus*).

2. The *Raceme.*—The main axis of the inflorescence elongated but the flowers borne on pedicels which are about equal in length. Examples: The hyacinth (*Hyacinthus*), cabbage (*Brassica oleracea*), and currant (*Ribes*).

3. The *Corymb.*—The main axis of the inflorescence elongated but the pedicels of the older flowers longer than those of the younger flowers so that the flowers are all in one plane, i.e., the inflorescence is flat-topped. Example: The cherry (*Prunus cerasus*).

4. The *Umbel.*—The axis of the inflorescence short and the flowers upon pedicels of nearly equal length. Example: The onion (*Allium*).

5. The *Head.*—The axis very short and the flowers sessile (without pedicels). Examples: The thistle (*Cirsium*), sunflower (*Helianthus*), and other members of the *Compositae.* (In this family each so-called flower is an inflorescence of many small true flowers.)

II. **Compound Racemose Inflorescences.**—The main axis branched and each branch bearing a group of flowers.

1. The *Panicle.*—The branches of the axis bearing loose racemose flower cluster. Examples: The oat (*Avena*) and the Spanish bayonet (*Yucca*).

2. The *Compound Spike.*—The branches of the axis are spikes. Examples: Wheat (*Triticum*) and rye grass (*Lolium*).

3. The *Compound Umbel.*—The axis much shortened and its branches arranged like an umbel, each branch itself bearing an umbel. Examples: The carrot (*Daucus*), the parsnip (*Pastinaca*) and most other members of the family *Umbelliferae.*

In addition to the inflorescences mentioned there are a number of mixed inflorescences in which cymose flower clusters are borne on racemose inflorescences and vice versa.

REPRODUCTION BY FLOWERS

In the higher plants, including cultivated plants of all kinds, the flower is the organ of sexual reproduction. It is in the flower that the seed is developed. We have learned that many plants may be reproduced by means of vegetative organs, such as stems, roots, and leaves. This method of reproduction is known as **asexual;** there is no union of protoplasts; it involves only multicellular portions which may be detached from the parent plant and develop into new plants. Reproduction by flowers, however, is a **sexual** method; in this, there is a fusion of two specialized protoplasts, from which union a new individual arises.

The principal steps in the development of the seed are as follows: pollination, growth of the pollen tube, fertilization, formation of the embryo and endosperm, and development of the ovule tissues outside of the embryo and endosperm. These will be discussed in the order given.

Pollination.—The transfer of pollen from the anther to the stigma is called **pollination.** The anthers of the stamens open when the pollen is mature and the pollen grains escape. In grass flowers and other flowers whose pollen is carried by the wind, the anthers are attached to the filaments in such a manner that air movements easily swing them back and forth. As a result, the pollen falls from the anthers and is launched into the air. The pollen grains, being small and light, may be carried considerable distances by a slight breeze. Some of the pollen grains, although relatively few compared to the great number which are lost and never function, thus reach the stigmas of flowers of the same species. The stigmas of such species are generally much branched and plume-like so that the chances of pollen coming into contact with them is greater than would otherwise be the case. In plants with relatively inconspicuous flowers, such as grasses, poplars, alders, birches, oaks, hickories,

nettle and hop, wind-pollination occurs. In a few cases water and birds are the agencies of pollination. In the majority of flowering plants, however, pollen transfer is accomplished by bees (which visit the open flowers to secure nectar for the making of honey or to get pollen for the feeding of the young bees in the hive), or by other insects. Such plants are said to be **insect-pollinated.** In insect-pollinated plants, the pollen does not fall from the opened anthers but sticks to the outside of the shrunken anthers until, through contact with the body of an insect, some of it is swept off and adheres to the insect. When the insect visits another flower some of this pollen may be rubbed off on the stigmas. Except in the case of certain nuts, insects are necessary for the pollination of most deciduous fruit trees.

Pollen may be transferred from an anther to the stigma of the same flower or to the stigma of another flower on the same plant, in both of which cases **self-pollination** is said to have taken place. If pollen is transferred from an anther to the stigma of a flower on another individual plant, it is spoken of as **cross-pollination.**

Some plants are normally self-pollinated. This is true of most cereals, except rye and corn, of garden pea, tobacco, cotton and other plants. In a great many species, however, cross-pollination is the rule, and their self-pollination may be attended by a reduction in vigor and productivity. Darwin in 1876 concluded from his rather extensive experiments in many plant families, that, in general, the plants resulting from cross-pollination excelled in vigor, weight, height and other characters those plants resulting from self-pollination. However, there are reasons for believing that the advantages of cross-pollination and disadvantages of self-pollination have been overdrawn.

One finds various means by which self-pollination is made difficult or impossible and cross-pollination is aided or insured. Among such means may be mentioned the following:

1. The anthers of a flower shed their pollen before the stigma of that flower is receptive (beet, *Beta*, and red clover, *Trifolium pratense*).

2. The stigmas mature and become incapable of pollination before the anthers open (common plantain, *Plantago* and avocado, *Persea*).

3. The pollen is not capable of germinating on the stigma of the same flower (rye, *Secale*).

4. The staminate and pistillate flowers are borne on different plants, (hemp, *Cannabis*, willow, *Salix*, date, *Phoenix*, and others). Such species have two kinds of individuals, staminate and pistillate. This is spoken of as **dioecism.**

5. The stigmas and anthers in different flowers occupy different levels. For example, in the Chinese primrose (*Primula sinensis*) there are

plants the flowers of which have long styles, and short stamens attached at the base of the corolla, and other plants whose flowers have short styles, and stamens attached toward the upper part of the corolla (Fig. 196). The level of the stigma in long-styled forms is approximately the same as that of the anthers in short-styled forms; and the level of the stigma in short-styled flowers is about the same as that of the anthers in long-styled flowers. An insect which visits one type of flower receives pollen on a part of its body which will be brought in contact with the stigma of the other type of flower, thus effecting cross-pollination.

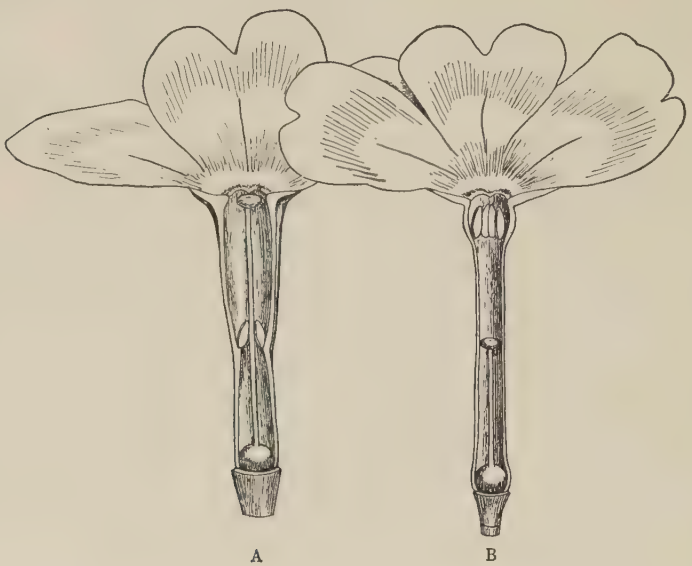


Fig. 196.—Flowers of a primrose showing heterostyly. *A*, long-styled form. *B*, short-styled form. (After Darwin.)

6. Toxic pollen. In certain orchids the pollen appears to actually cause a withering of the stigma of the same flower, but is potent on the stigmas of other flowers.

The mature pollen grain at the time it is discharged from the anther is a spherical or oval structure having two surrounding membranes, of which the inner is called the **intine** and the outer the **exine.** The intine is of cellulose and pectic substance, whereas the exine is largely of cutin. The exine is frequently covered with ridges, spines, or other sculpturings. In many kinds of pollen these form intricate and beautiful geometric designs upon the surface. The protoplasm of the pollen grain is dense and contains a large quantity of stored food. Vacuoles are generally

absent. About the time the pollen grain is shed, the single nucleus generally divides into two, the **generative nucleus** and the **tube nucleus.** These are not separated by a cell wall, but the cytoplasm surrounding the generative nucleus is generally distinctly differentiated from the rest of the cytoplasm of the pollen grain.

Formation of the Pollen Tube.—Pollen which reaches the stigma adheres there due to of the fact that the stigmatic surface is made up of short outgrowths, or papillae, which are, in many species, covered

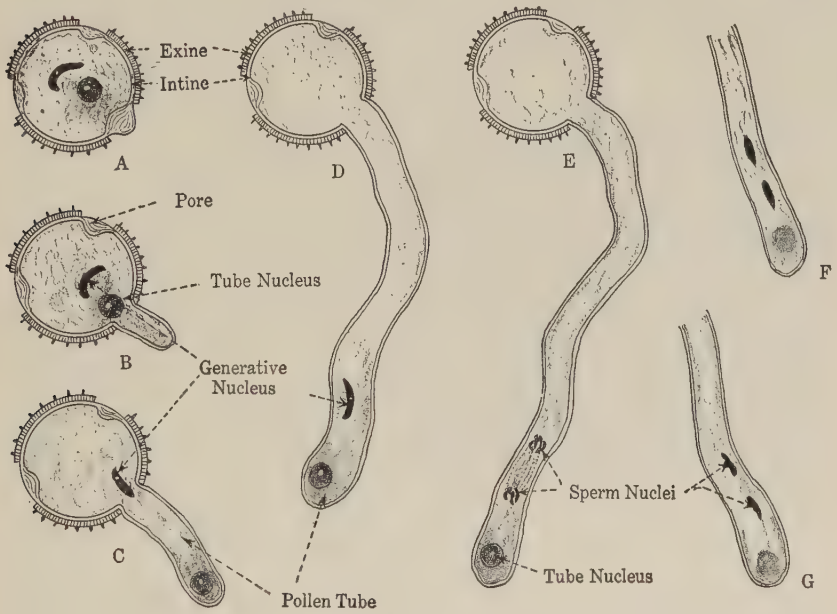


FIG. 197.—Stages in the germination of the pollen grain, and development of the pollen tube. (Redrawn from Bonnier and Sablon.)

by a sticky secretion, the **stigmatic fluid.** Soon after pollination the protoplasm absorbs water and swells, breaking the exine. The intine is stretched and extends through the break in the outer wall, forming a tube, the pollen tube, which penetrates the tissue of the stigma and grows down through the style and enters the ovary. The pollen of a great number of common plants can be artificially germinated by placing the grains in a sugar solution of proper concentration or in some cases merely in water. In a few flowers with hollow styles, it is not necessary that the pollen tube actually penetrate the stylar tissue. In most flowers, however, enzymes are secreted at the tip of the tube, the stylar tissue is dissolved away, and thus a passage is made for the advance

of the tube. When the pollen grain germinates, vacuoles appear in the protoplasm. Soon the generative nucleus undergoes division, forming two nuclei, the so-called **sperm nuclei** or **male nuclei.** The two male nuclei and the tube nucleus, together with most of the cytoplasm, pass to the tip of the tube and remain there as the tube advances. In some flowers the style is very short and the tube has only a short distance to grow. For example, in the calla lily (*Richardia*), or beet (*Beta*), the distance from the surface of the stigma to the ovary is only 2 or 3 millimeters. In certain other flowers the pollen tube must grow to a great length before the ovary is reached. This is the case in Indian corn (*Zea mays*) in which the distance from the stigma at the end of the corn silk to the attachment of the silk (style) to the young corn grain (ovary) may be as much as 45 centimeters.

FIG. 198.—Pollen grains of various forms and markings. (After Kerner.)

There are wide differences in the rate of growth of the pollen tube. Thus in the autumn crocus (*Colchicum autumnale*) the tube takes six months or more to grow the length of the style which is only a few centimeters; and in some oaks the tube is almost a year in growing two or three millimeters. On the other hand, in the true crocus (*Crocus*) the tube may grow 10 centimeters or more down to the ovary, in three days.

Fertilization.—The structure of the ovule and of the embryo sac within it has already been described (page 244). It will be recalled that the fully developed embryo sac consists of a vacuolated mass of cytoplasm containing eight nuclei: three antipodal nuclei, two polar nuclei, two synergids, and one egg nucleus (Figs. 172 and 180).

When the pollen tube reaches the ovary it grows toward one of the ovules and enters the embryo sac, generally through the micropyle and nucellus. In some species, however, it reaches the embryo sac by piercing the integuments or the base of the ovule. After entering the embryo sac the wall at the tip of the pollen tube breaks and its cytoplasm and the three nuclei are discharged into the sac (Fig. 400). Then one of the male, or sperm, nuclei moves toward the egg or female nucleus and fuses with it. The fusion nucleus or fertilized egg nucleus and asso-

ciated cytoplasm is called the **zygote.** The second male, or sperm, nucleus passes to the center of the sac, where it fuses with the polar nuclei, or with a single nucleus in case these have previously united. The nucleus thus resulting from the fusion of the three nuclei is called the **primary endosperm nucleus.**

The union of the egg nucleus with one of the male nuclei and of the other male nucleus with the polar nuclei is spoken of as **double fertilization.**

Formation of the Embryo.—Shortly after the fertilization of the egg cell, the fusion nucleus, together with some of the cytoplasm of the sac, becomes surrounded by a cell wall. Then follows a series of cell divisions, resulting in the formation of a mass of cells which develops into the rudimentary plant or **embryo** of the seed. This embryo grows into a new plant when the seed germinates. Figure 199 shows a number of stages in the development of the embryo from the zygote.

Formation of the Endosperm.—Shortly after fertilization, the primary endosperm nucleus undergoes repeated divisions which are not, however, attended by the formation of cell walls. The cytoplasm of the embryo sac meanwhile increases in amount as food is supplied from the surrounding tissue of the ovule. The numerous endosperm nuclei and this cytoplasm come to line the embryo sac and finally may fill the whole sac, except for the space occupied by the developing embryo. Sooner or later there is an almost simultaneous formation of cell walls between all the endosperm nuclei so that there results a mass of tissue called the **endosperm.**

Fate of the Synergids and Antipodal Nuclei.—In many plants, one or both of the synergids are destroyed by the pollen tube as it enters the embryo sac. The antipodal nuclei, which in some plants are surrounded by walls even before the pollen tube enters the embryo sac, may persist for some time. In some species they increase in number, apparently serving to absorb food for the embryo sac from the tissue at the base of the ovule. These cells, and the synergids as well, sooner or later undergo disorganization, their protoplasm being utilized as food for the development of the endosperm or embryo.

Further Development of the Seed.—Fertilization stimulates the tissues outside the embryo sac to active growth so that the whole ovule increases greatly in size. Thus the seed may grow to be hundreds of times as large as the unfertilized ovule. In addition to increasing in number, the cells of one or both integuments of the ovule undergo great changes in the nature and thickness of their cell walls, and thus the **seed coats** are formed. The nucellus generally disappears before the seed is fully developed. It may, however, as in certain water lilies,

make up a large part of the seed. The endosperm grows actively, at least during the early part of the seed's development. In some plants, such as the bean (*Phaseolus*), pea (*Pisum*), and other legumes, the endosperm is entirely used up by the embryo before the seed ripens. In such cases the mature seed consists only of an embryo and one or more seed coats. In other species (all grasses, for example) much of the endosperm remains even in the ripe seed. It is then available as a source of food for the embryo during germination.

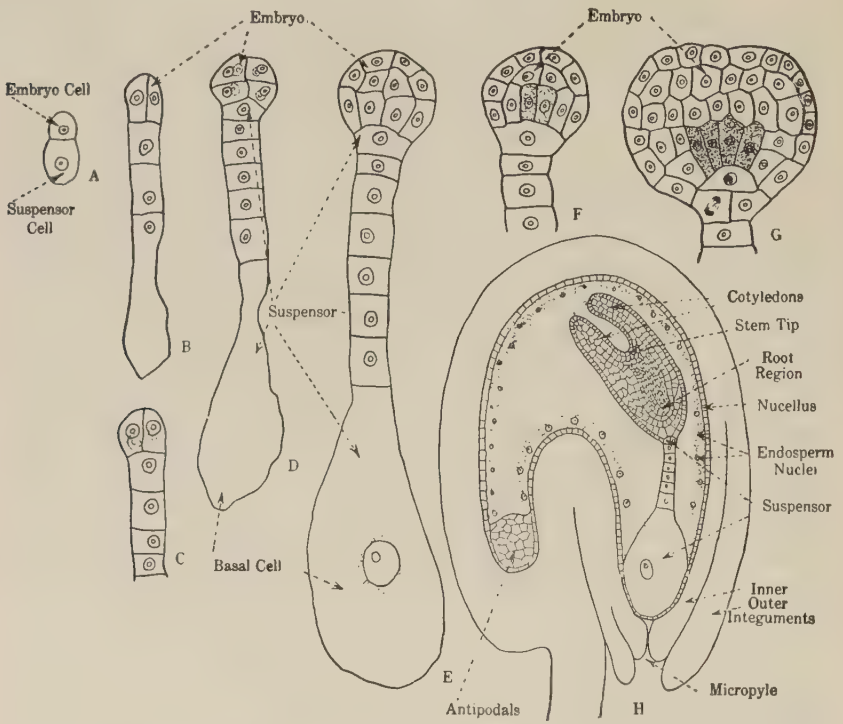


FIG. 199.—Stages in the development of the embryo of shepherd's purse (*Capsella*) a *dicotyledonous* plant. (*A–G*, redrawn from Coulter and Chamberlain); *H*, redrawn from Bergen and Caldwell.)

Effect of Fertilization on Fruit Formation.—The effect of fertilization generally extends to the ovary and starts growth and differentiation of its cells, thus resulting in fruit formation. In the apple, pear, and several related plants, the receptacle is also stimulated to growth and takes part in the formation of the fruit. There are, however, many plants in which fruit formation takes place even though fertilization does not occur. Such development of the fruit without fertilization is called **parthenocarpy.**

SUMMARY OF THE PROCESS OF REPRODUCTION BY FLOWERS

The Structures Involved:

(*a*) Pistil with the ovary, style and stigma.

(*b*) Ovule or ovules in the ovary.

(*c*) Mature embryo sac in each ovule, consisting essentially of cytoplasm and 8 nuclei, as follows:

(1) Two synergids or helper-nuclei.

(2) One egg nucleus.

(3) Two polar nuclei.

(4) Three antipodal nuclei.

(*d*) Stamens, each with filament and anther.

(*e*) Pollen grains in the anther, each generally containing when shed, 2 nuclei, as follows:

(1) One tube nucleus.

(2) One generative nucleus.

The Process:

(*a*) The transfer of pollen from an anther to the stigma (pollination).

(*b*) Germination of the pollen grain on the surface of the stigma, and growth of the pollen tube through the tissue of the stigma and style to the ovule, where it passes through the micropyle and penetrates the nucellus, thus entering the embryo sac. The generative nucleus divides into two sperm nuclei.

(*c*) Dissolution of the tip of the pollen tube and discharge of the tube nucleus and two sperm nuclei into the embryo sac.

(*d*) Fusion of one sperm nucleus with the egg nucleus to form the zygote (fertilization).

(*e*) Fusion of the other sperm nucleus with two polar nuclei, to form the primary endosperm nucleus (fertilization).

(*f*) Disorganization sooner or later of the tube nucleus, the synergids and the antipodal nuclei.

(*g*) Development of the embryo from the zygote.

(*h*) Development of the endosperm tissue from the primary endosperm nucleus.

(*i*) Further development of the seed, including

Growth of the embryo.

Growth (or absorption) of endosperm.

Disappearance (usually) of nucellus.

Development of integuments into seed coats.

(*j*) Loss, or at least death of, stigma, style, stamens, petals and sometimes of sepals.

(*k*) Development of ovary (sometimes also of part of sepals and receptacle) into fruit.

CHAPTER VIII

FRUIT AND SEED

THE FRUIT—INTRODUCTION

Fruits, including the seeds which they contain, constitute the most important source of man's food supply. Although the stem of the sugar cane and the root of the sugar beet furnish most of the sugar we use, and although the tuber of the Irish potato and the roots of the sweet potato, turnip, and carrot are important elements in our diet, there can be no doubt that fruits and seeds are, of all plant parts, the most important as food sources. Such fleshy fruits as apples, plums, peaches, cherries, oranges, grapes, and figs are valuable arrticles of diet on account of their content of sugar and fruit acids. Without question, wheat and rice are the two most important items in the world's food supply and these and the other grains, such as corn, barley, and rye, are actually one-seeded fruits, although it is only the material of the seed itself which the human body is able to digest and absorb as food.

The origin and improvement of cultivated fruits forms a most interesting chapter in the history of agriculture. Our present-day fruits in all their variety, adapted as they are to many different soils and climates and suited to the tastes of many people, have been derived from wild plants, which in their primitive state yielded fruits of inferior quality.

In the botanical sense, a fruit is a matured ovary of a flower, including its one or more seeds and any part of the flower which may be closely associated with the ovary. This definition would include such one-seeded, dry fruits as corn, oats, wheat, and other cereals, which are commonly spoken of as " seeds ", as well as tomatoes, the pods of beans and peas, walnuts and acorns, and many other structures which are not fruits in the popular sense.

THE DEVELOPMENT OF THE FRUIT

As already stated in our discussion of the flower, the immediate result of fertilization is the initiation of a series of changes in the embryo sac and ovule, which lead to the development of the seed.

Normally, these are followed by changes in the surrounding ovary tissue, and often in other adjacent flower structures, resulting in what is popularly called " setting " of the fruit. Thus, the stimulus of fertilization, the nature of which is not well understood, extends its influence not only to the ovule, but to the ovary as well, and in some cases beyond the ovary to include tissue of other flower parts. In the great majority of plants, fruit does not form unless pollination is followed by fertilization and this by normal seed development.

In most fruits there is rather close correlation between the number of seeds formed and the size, form and even the composition of the fruit. For example, seedless fruits of the date palm are much smaller than those containing seeds; and in grapes, there is a close relation between the number of seeds and the weight of the flesh, those grapes which have the greatest number of seeds generally being the largest. It is a common observation that, as in the case of the tomato, locules which do not contain a number of good seeds are not well developed and fruits with such locules are irregular and distorted in form. Similarly, apples that are extremely one-sided will usually be found to have no seeds in the less-developed side, whereas seeds are present in the large side. It has been shown that seedless pears are not so rich in sugar and in acid as those containing one seed, and these in turn contain less of these substances than do those having more than one seed.

However, in many plants, fruit development takes place without seed formation, and without the processes (pollination and fertilization) which must normally precede seed development.

The term **parthenocarpy** is applied to all those cases of fruit development which occur in the absence of fertilization. Such fruits are practically always seedless, in which case they are frequently distinctly different in size and form, from fruits of the same variety which contain seeds (Fig. 200). Very rarely, however, seeds may develop parthenogenetically (without fertilization) in parthenocarpic fruits. Moreover, not all seedless fruits are parthenocarpic, for seedlessness may be due to abortion of the embryos after fertilization rather than to absence of fertilization.

A number of our cultivated plants regularly bear parthenocarpic fruits, which are seedless. Among these may be mentioned seedless raisin grapes (chiefly Sultanina and Black Corinth varieties), English forcing cucumber, certain varieties of egg plants, navel oranges, the banana, the pineapple, and some varieties of apples and pears.

It has been found that in some cases mere pollination without subsequent fertilization may be sufficient to start fruit development. In certain orchids, fruit development may be initiated by placing dead

pollen or a water extract of pollen upon the stigma. Even pollen from a plant belonging to another genus may bring about fruit formation, as in the case of certain varieties of European grapes (*Vitis*) pollinated by the pollen of Virginia Creeper (*Parthenocissus*). In none of

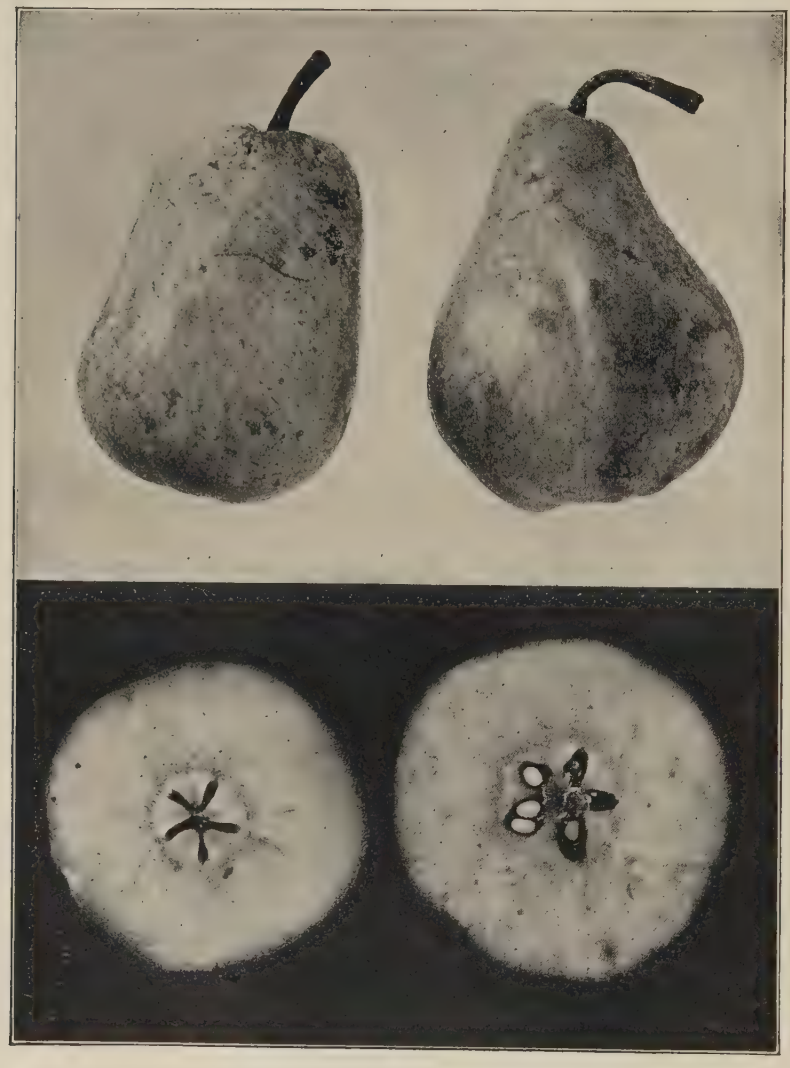


Fig. 200.—Bartlett pears (left), self-pollinated; right, cross pollinated with Winter Nelis. Bartlett pears in certain sections of California are self-sterile but may develop parthenocarpic fruit, as shown in the figures at the left. Note the abnormal shape of the parthenocarpic fruit and the absence of seeds in the locules. (From Division of Pomology, College of Agriculture, University of California.)

these cases of parthenocarpy, nor in various others that might be cited, does fertilization take place.

Structurally, the ovary walls are relatively simple, being largely made up of parenchyma cells. The structure of the fruit wall or **pericarp,** into which they develop, however, is sometimes quite complex. Three distinct layers are generally present in the pericarp. Named in order, beginning with the outermost, these are the **exocarp, mesocarp** and **endocarp.**

The exocarp of the mature fruit varies widely in structure in different types of fruit. It usually consists of a single layer of cells,

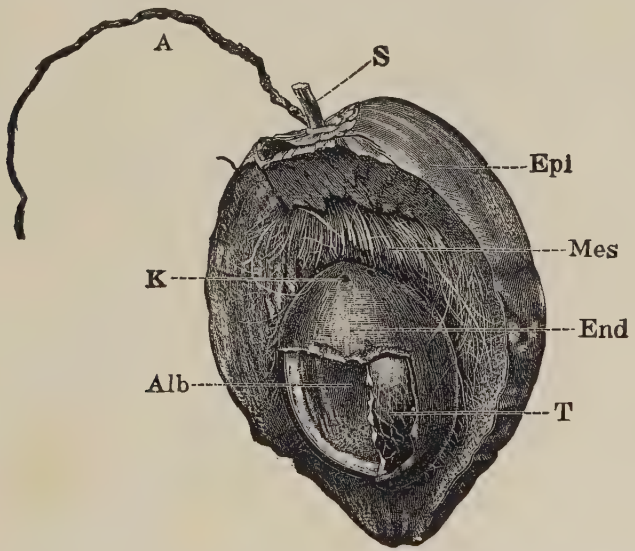


FIG. 201.—The fruit of cocoanut (*Cocos nucifera*). *S*, lower part of axis forming the stem; *A*, upper end of axis with scars of male flower; *Epi*, exocarp; *Mes*, mesocarp; *End*, endocarp; *T*, portion of nucellus adhering to endosperm; *Alb*, endosperm surrounding cavity of the nut; *K*, germinating "eye." (After Winton.)

which constitutes the epidermis. Hairs are often present, as are also stomata.

The mesocarp in some fruits forms a very thin layer, whereas in others it may be as much as several centimeters thick.

The endocarp may consist of a single cell layer, constituting an inner epidermis of the pericarp, as in the fruit of buckwheat (*Fagopyrum esculentum*), or it may be composed of a number of cell layers variously modified, as in the fruit of the plum, cherry, and other stone fruits.

A fruit, botanically, is the matured ovary, with its seeds, and any parts of the flower which may be closely associated with it. The seed is the matured ovule. The fruit contains the seed or seeds. For example, the entire bean pod is a fruit; the beans within are the seeds. It is particularly in the dry, one-seeded fruits that there is need of a clear distinction between fruit and seed. For example, the buckwheat fruit (akene) and grass fruit (grain) are commonly called " seeds," but if their development is followed through, and their structure carefully studied, they are found to be true fruits, having a very thin pericarp (ovary wall) surrounding a single seed.

CLASSIFICATION OF FRUITS

Though most fruits consist of only a single ovary there are some, including a number of the most important cultivated ones, which consist of or include several ovaries. In some of these cases the several ovaries are from a single flower and in others they are from several very closely clustered flowers.

On the basis of the number of ovaries involved in their formation fruits may be classified thus:

Simple—consisting of a single enlarged ovary, with which some other flower parts may be incorporated. Most common fruits are simple fruits except those listed below as examples of aggregate and multiple fruits.

Aggregate—consisting of a number of enlarged ovaries belonging to a single flower and massed on or scattered over the surface of a single receptacle. The separate ovaries are spoken of as fruitlets. Examples: raspberry, blackberry, and strawberry.

Multiple—consisting of the enlarged ovaries of several flowers more or less coalesced into one mass. Examples: mulberry, fig and pineapple.

Simple fruits, on the basis of their consistence, structure and dehiscence may be classified as follows:

I. **Fleshy Fruits** (pericarp fleshy).

A. Berry—the ovary wall fleshy and enclosing one or more seeds. Examples: grape, gooseberry, currant, pepper, tomato, and date.

(*a*) *Pepo*, a type of berry with hard rind. Examples: squash or cucumber.

(*b*) *Hesperidium*, a type of berry with a leathery rind. Examples: orange and lemon.

B. Drupe or stone fruit—one-seeded; exocarp thin forming the skin; mesocarp fleshy; endocarp stony. Examples: cherry, peach, almond, plum, and olive.

C. Pome—receptacle fleshy; outer portion of pericarp fleshy; inner portion papery, forming "core." Examples: pear, apple and quince.

FIG. 202.—Fruits of common plants, illustrating, with the exception of *F*, the principal methods of dehiscence. *A*, pod of pea (*Pisum sativum*). *B*, silique of mustard (*Brassica*). *C*, capsule of Jimson weed (*Datura*), septicidal dehiscence. *D*, three follicles of larkspur (*Delphinium*). *E*, samara of maple (*Acer*). *F*, aggregate fruit of raspberry (*Rubus*). *G*, capsule of violet (*Viola*), loculicidal dehiscence. *H*, capsule of poppy (*Papaver*) poricidal dehiscence.

II. **Dry fruits** (pericarp dry).

A. Dehiscent fruits (splitting open when ripe).[1]

(*a*) Legume or true pod—carpel one; splitting along two sutures. Examples: pea, bean, vetch.

(*b*) Follicle—carpel one; splitting along one suture. Examples: milkweed, larkspur, columbine, peony.

[1] Except the silique of a single genus (*Raphanus*) of the Cruciferae.

(*c*) Capsule—carpels two or more; dehiscing in one of three different ways:

1. Along line of union (septicidal)—azalea.
2. Along middle of carpel (loculicidal)—iris, lily.
3. By pores (poricidal)—poppy.

(*d*) Silique—carpels two; separating at maturity, leaving a partition wall persistent—crucifers.[1]

B. Indehiscent (not splitting open when ripe).

(*a*) Akene—one seeded; seed attached to ovary wall at one point only. Examples: buckwheat, sunflower, buttercup.

(*b*) Caryopsis (grain)—one-seeded; pericarp firmly united to testa or seed coat. Examples: wheat, corn, rice, barley, broom corn, oats and all other grasses.

(*c*) Samara or "key" fruit—one or two-seeded; pericarp modified, being a wing-like outgrowth, extending about seed. Examples: ash, elm, maple.

(*d*) Schizocarp—carpels two or more; united, splitting apart at maturity. Examples: carrot, parsnip, parsley, celery, mallow.

(*e*) Nut—a hard, one-seeded fruit, generally resulting from a compound ovary.

Simple Fruits.—The fruits of the great majority of flowering plants are simple fruits, each arising from a single ovary. The principal types of simple fruits have been mentioned in the classification given and will be discussed later in this chapter.

Aggregate Fruits.—An aggregate fruit is one composed of a single receptacle upon which are massed many similar true fruits. It is derived from a single flower having many pistils. The various kinds of aggregate fruits differ in the type of individual fruits which make up the aggregate. For example, in the dewberry, raspberry, blackberry and other species of *Rubus*, the individual fruits of the aggregate are drupes and constitute the pleasant-flavored portion of the fruit; in the dewberry and blackberries, the drupelets adhere firmly to the receptacle, while in raspberries the drupelets easily separate from the receptacle when the fruit is picked and cling together in the form of a cup (Fig. 203.) In the strawberry (*Fragaria*) they are akenes, and it is the receptacle which gives the characteristic flavor.

As shown in the diagram of a lengthwise section (Fig. 204) of the

[1] Except the silique of a single genus (*Raphanus*) of the Cruciferae.

ripened fruit, the receptacle consists of a fleshy pith and cortex with vascular bundles between them. The persistent calyx and withered stamens are at the base of the fruit and constitute the "hull." The akenes are generally spoken of as "seeds."

Multiple Fruits.—Whereas an aggregate fruit, as we have just learned, is derived from a single flower having many pistils, the multiple fruit is developed from the ovaries of many separate and yet closely clustered flowers. Among the most familiar examples of plants bearing multiple fruits are the mulberry (*Morus*), pineapple (*Ananassa sativa*), and fig (*Ficus*). In the mulberry there are staminate and pistillate flowers, and they occur in separate inflorescences. Staminate inflorescences soon fall after the flowers have shed their pollen. The pistillate flowers are crowded together to form a dense inflorescence. Each flower possesses a single, one-celled ovary. Each ovary develops into a nutlet which is enclosed by the thickened, juicy calyx lobes. Finally, the separate fruits become crowded together and somewhat coalesced to form a multiple fruit, the mulberry.

FIG. 203.—The aggregate fruit of blackberry (*Rubus* sp.). Each so-called "fruit" is an aggregate of drupelets. (From Division of Pomology, College of Agriculture, University of California.)

The flowers of the fig line the inner wall of an enlarged, fleshy hollow receptacle. Staminate and pistillate flowers may be borne in the same or in different receptacles. Each pistillate flowers has a single one-celled ovary, which develops into a nutlet. These nutlets are imbedded in the inside of the wall of the fleshy receptacle. The succulent receptacle, together with the enclosed nutlets derived from a number of flowers, is the "fig." This type of multiple fruit is sometimes called a **synconium.** In the common edible fig (Mission fig) the receptacle comes to maturity without fertilization of the enclosed pistillate flowers. However, in Smyrna and several other types of figs, the proper ripening

of the receptacle must be preceded by fertilization of the pistillate flowers and the development of the ovaries and seeds.

In the pineapple (*Ananassa*) there is a central axis which is the axis of the inflorescence from which the multiple fruit develops. Growing out from this elongated central portion are numerous sessile flowers, the fleshy bases and ovaries of which are fused to form the outer part of the pineapple.

Fleshy Fruits.—*Berry.*—This is a true fruit possessing numerous seeds wholly or partly embedded in a fleshy endocarp and mesocarp. The tomato is a common example of a berry. Whereas the wild form of our common garden tomato (*Solanum esculentum*) has a two-celled fruit with a relatively dry placenta, cultivated forms of the common garden tomato have a large number of locules in the fruit, in which the placentae are exceedingly fleshy. The pear and cherry tomatoes both have two-celled fruits, and on that account these types are regarded as being nearest the original type. There are numerous varieties of tomatoes, the fruits of which vary in color, shape, and character of the surface. The tomato bears numerous, small seeds.

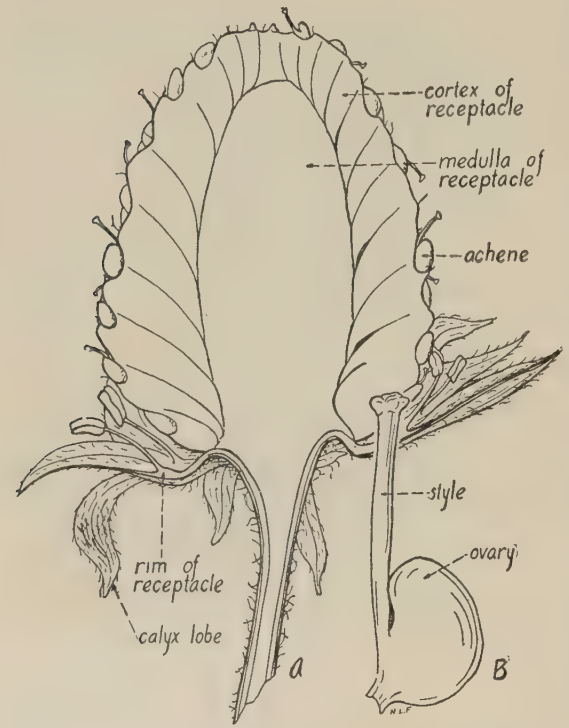


FIG. 204.—The aggregate "fruit" of strawberry (*Fragaria*). *A*, the "fruit" in median lengthwise section; *B*, single akene. (After Robbins, from *Botany of Crop Plants.*)

Another familiar berry is the grape (*Vitis*). It has a smooth epidermis, often covered with a waxy secretion (" bloom "). In Old World grapes (*Vitis vinifera*), including such varieties as Muscat and Malaga, the exocarp (" skin ") of the mature berry does not separate freely from

the mesocarp ("pulp"). In American grapes, such as the Concord variety, on the other hand, the exocarp separates readily from the mesocarp.

The date is a berry, for its "stone" is actually the seed and not stony endocarp as in the drupes of peaches, plums, etc.

The fruits of oranges, lemons, limes, and grapefruit are berry-like. This type of fruit is sometimes termed a **hesperidium.** It is made up of a thick, leathery rind (pericarp) with numerous oil glands, and a juicy pulp composed of numerous cells. In the common sweet orange (*Citrus sinensis*) there are normally ten two-seeded locules. However, the number of locules and seeds may vary. There are a number of seedless varieties, such as the navel orange. In these, the fruit is parthenocarpic.

The **pepo** is a berry-like fruit, the outer part of which is receptacle which has become attached to the exocarp (Fig. 205). The flesh of the fruit is principally mesocarp and endocarp. The pepo is the type of fruit characterizing the Cucurbitaceae which include the watermelon, squash, pumpkin, cantaloupe, cucumber, etc. In the Turban squash (a variety of *Cucurbita maxima*) the fruit has the appearance of a turban. This is because the fleshy receptable does not completely cover the ovary, and hence the latter protudes. The character of the resulting fruit has suggested the expression "squash within a squash."

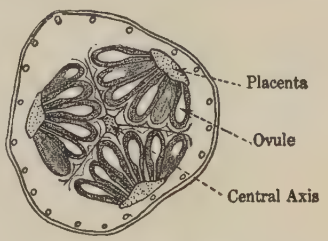


FIG. 205.—Cross section of a mature fruit (pepo) of cucumber (*Cucumis sativus*). (After Robbins, from *Botany of Crop Plants.*)

Drupe.—This type of fruit is characteristic of the plum family (*Drupaceae*). The family includes the plum, cherry, almond, peach, and apricot, which are popularly known as the "stone fruits." The almond fruit is considered to be a drupe though the mesocarp, fleshy like a typical drupe when immature, becomes dry and hard as the fruit develops, splitting at maturity. The olive fruit is also a drupe. As is noted in the classification, the drupe is one-seeded but, if one examines the young ovary of a *Prunus* flower, two ovules will be found, one of which usually fails to develop into a seed. The most characteristic thing about the drupe is that the single seed is surrounded by a hard endocarp consisting of very thick-walled stone cells.

Pome.—This is a fleshy, many-seeded fruit in which the receptacle comes to form a large amount of the flesh of the fruit. The pome type of fruit occurs in the apple family (*Pomaceae*), which includes such

well-known plants as apple (*Malus*), pear (*Pyrus*), and quince (*Cydonia*).

In the median cross section of the apple fruit (Fig. 208), the relation of carpels and receptacle is clearly shown. Each of the five carpels is composed of a parchment-like endocarp, a fleshy mesocarp, and a fleshy exocarp. There are no vascular bundles in the pith. Normally, there are ten primary vascular bundles seen in the median cross section. They are adjoined on the inside by the pith, and on the outside by the cortex of the receptacle.

FIG. 206.—The mature fruit (drupe) of the almond (*Prunus amygdalus*). The tough leathery hull composed of exocarp and mesocarp is shown splitting from the endocarp which is pitted, and which encloses the seed. (From Division of Pomology, College of Agriculture, University of California.)

In a longitudinal section (Fig. 208) the flesh is seen to be separated into two parts by a distinct line, which is called the **core line.** Inasmuch as the primary vascular bundles of the receptacle follow the core line, this line marks the limits of the pith and the cortex. Branches of the primary bundles spread out into the cortex of the fruit.

Dry Dehiscent Fruits.—*Legume or True Pod.*—This is the type of fruit which characterizes nearly all members of the pea family (*Leguminosae*). The ventral suture of the bean or pea pod, for example, is

the one along which the edges of the carpels are fused together and also along which the seeds are attached, and the dorsal suture corresponds to the midrib of the carpel. In the bean or pea pod, the " shell " is the pericarp, and the " beans " or " peas " are the seeds. In medicks (*Medicago* species) the pods are spirally twisted or curved and may be smooth (alfalfa, *Medicago sativa*) or spiny (bur-clover, *Medicago hispida*).

Follicle.—The follicle differs from the legume or true pod, which opens along two sutures, in that the single carpel opens along one suture.

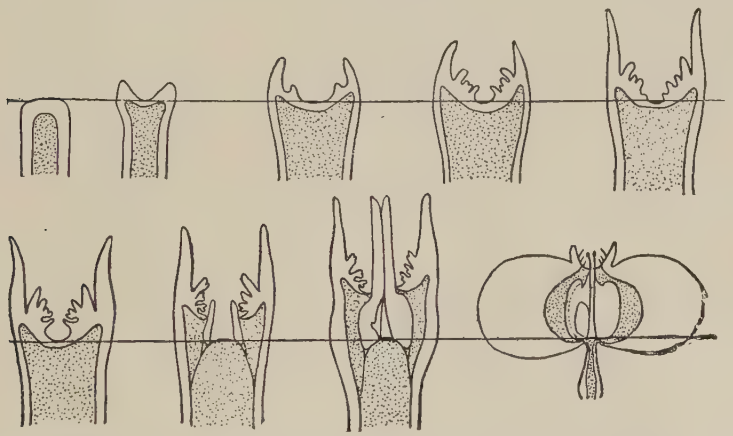


FIG. 207.—Diagrams showing the development of the apple flower and fruit. Dotted areas represent the pith of the receptacle. Successive stages are shown from left to right. The primordia of the sepals appears first. The receptacle becomes concave, the margin continuing to grow during the development of the flower parts. Following the appearance of the sepal primordia, the primordia of the petals are formed, then those of the stamens, and lastly the primordia of the carpels which later fuse to form a compound pistil. In the mature flower the ovary is completely buried in the tissue of the receptacle. After pollination the tissue of the receptacle which surrounds the ovary grows very actively so that it makes up a much larger part of the fruit than does the ovary (core). (After Kraus.)

Capsule.—When the carpels of a dry dehiscent fruit (capsule) split down the middle line as they do in lilies (*Liliaceae*), the dehiscence is said to be loculicidal. When the carpels open along the line of their union, as in *Rhododendron* and *Azalea*, the dehiscence is spoken of as septicidal. When the carpels open by pores. as in the poppy (*Papaver*), the dehiscence is said to be poricidal.

Silique.—The silique is a dry fruit derived from a superior ovary consisting of two carpels. This is the type of fruit characteristic of

the members of the mustard family (*Cruciferae*). The sides (valves) or walls of the ovary separate at dehiscence, leaving the two placentae and a thin partition (Fig. 202, *B*). This partition is formed during the de-

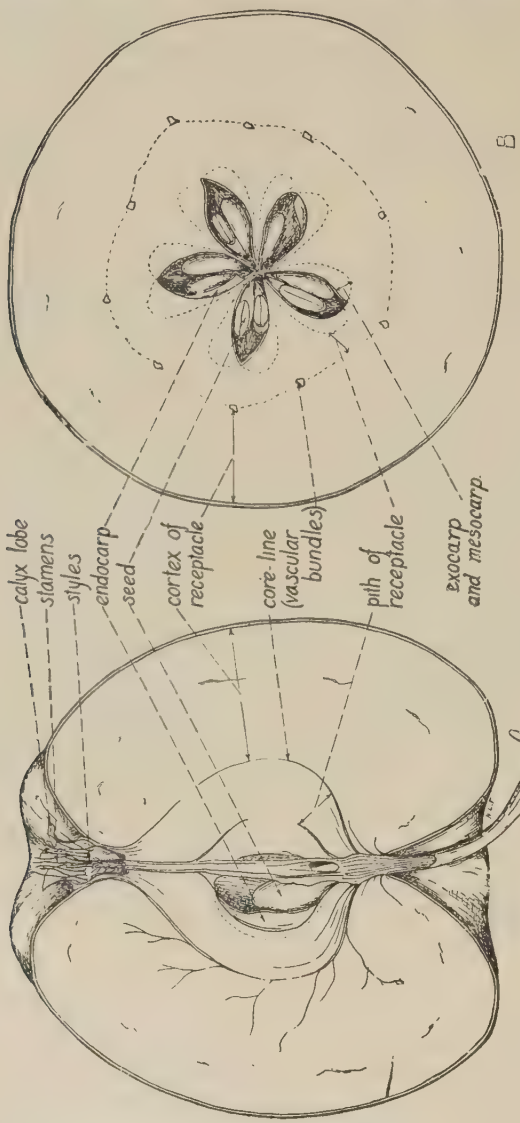


FIG. 208.—The mature apple fruit (pome). *A*, median longitudinal section. *B*, cross section. (After Robbins, from *Botany of Crop Plants*.)

velopment of the fruit by tissue outgrowths extending from the edges of the carpels inward. Finally by the meeting and fusion of these outgrowths a continuous partition results. In a few genera of mustards (*Raphanus*, radish, for example), the fruit is indehiscent.

The silique is elongated in radish (*Raphanus sativus*) and in the various species of the genus *Brassica*, including cabbage, turnip, rutabaga, rape, black and white mustards; it is much shortened, being about as broad as it is long, in shepherd's purse (*Capsella bursa-pastoris*), penny cress (*Thlaspi*), and others.

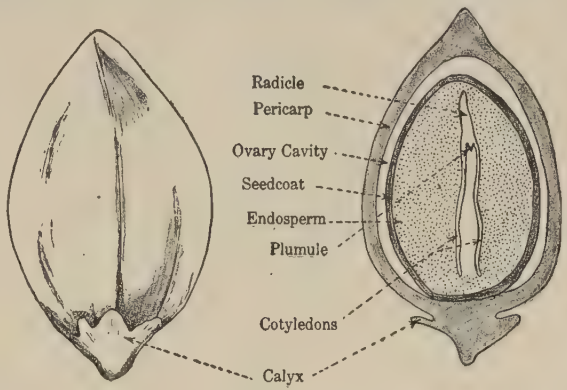


FIG. 209.—The fruit (akene) of buckwheat (*Fagopyrum esculentum*). External view (left), median longitudinal section (right.)

Dry Indehiscent Fruits.—Akene.—The buckwheat fruit (Fig. 209) is an excellent example of an akene. It is triangular; the point of the akene is the stigmatic end, while the opposite end shows a fragment of the flower stalk (pedicel) and small, persistent, withered calyx lobes which have become adherent to the pericarp. The "hull" of the buckwheat fruit consists of the pericarp together with the remains of the calyx.

Grain or Caryopsis.—The grain is the characteristic fruit of the grass family (*Gramineae*). A detailed account of the grain will be given in the discussion of seeds.

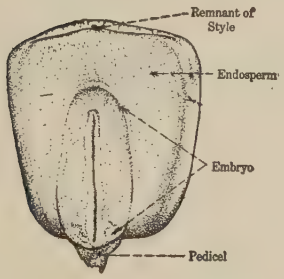


FIG. 210.—Fruit (grain) of corn (*Zea mays*), external view. The small projection at the upper end of the grain is the base of the style (strand of corn silk).

FIG. 211.—Acorn (nut) of oak (*Quercus*).

Samara.—In the samara or "key" fruit, the ovary wall is expanded to form wings, which aid the seed in its dissemination (Fig. 202, *E*). In the maple flower, for example, the ovary is two-celled and each cell has two ovules, only one of each developing into a seed. The outer and upper angle of each cell extends into a **wing.** The ovaries and wings enlarge considerably following fertilization. At maturity this double samara splits into two half-fruits.

Schizocarp.—This is the characteristic fruit of the carrot family (*Umbelliferae*). It is a dry fruit of two carpels, which separate at maturity along the midline into two one-seeded halves each of which is indehiscent.

Nut.—Typical fruits of this kind are entire ovaries the walls (pericarps) of which become hard throughout but do not dehisce. Examples of such typical nuts are acorn, chestnut and hazelnut. Many structures which are ordinarily called nuts do not correspond to the definition given. Thus the almond is the stone of a drupe and the walnut also is to be considered strictly speaking as a part of a drupe since its shell corresponds to the inner part only of the ovary wall, the outer part being fleshy in nature. A horse chestnut consists of a seed only, as does a Brazil nut.

THE SEED

Seeds are useful to man in a great many ways. He uses them as a means of multiplying useful plants. Seeds also furnish him with a large proportion of his food. The seeds of wheat and rice are the principal items of diet for hundreds of millions of human beings, in fact for a great part of the world's population. Second in importance to these great staple foods are the other cereals, such as corn, rye, and barley, and the seeds of various beans, particularly the soybean, which is an important article of diet among the Chinese. Many products used in the industries are also secured from seeds. Perhaps the most important of these are the various oils and fats produced from the seeds of such plants as the coconut (*Cocos nucifera*), cotton (*Gossypium*), flax (*Linum*), castor oil plant (*Ricinus communis*), and peanut (*Arachis hypogœa*). From the dried endosperm of the coconut, which is the material known as " copra," an oil is pressed which is used in the manufacture of substitutes for butter and lard, of soap and various other products. Cottonseed oil is a product of great commercial importance as is the oil pressed from the seeds of the peanut. These oils are used for purposes similar to those for which coconut oil is used. They and corn oil are also used for salad oil. The seed of flax yields an oil known as linseed oil, which is used in the manufacture of paints, varnishes, artificial leather, oilcloth and linoleum. The vegetable ivory of commerce, from which great numbers of buttons are made, is secured from the seed of the South American palm (*Phytelephas*). Many other kinds of seeds furnishing important commercial products might be cited.

THE DEVELOPMENT OF THE SEED

Following fertilization, the ovule begins to undergo the changes which result in seed formation. Every seed consists of at least two

parts, (1) the **embryo** and (2) the **seed coat** or **seed coats.** A third part called the **endosperm** is frequently present. It is enclosed, together with the embryo, within the seed coats. The embryo develops from the zygote, which is formed by the union of the egg or female nucleus of the embryo sac with one of the sperm or male nuclei of the pollen tube. The endosperm develops from the cell which is the result of the union of the polar nuclei of the embryo sac with the second sperm nucleus of the pollen tube. The integuments of the ovule become the seed coats.

As the embryo and endosperm develop, they do so at the expense of the nucellus. Part of the nucellar tissue is digested and supplies food for the developing embryo and endosperm. As a result, the nucellus in the mature seed is usually represented by a thin layer of cells, generally much compressed, just within the seed coats.

In the following outline there are shown the structures into which the various flower parts develop as the fruit and seed are formed.

Flower.				Mature Fruit and Seed.
Calyx				Adherent or deciduous
Corolla				Usually deciduous
Stamens				Usually deciduous
Pistil	Stigma			Withers; remnant may be present
	Style			Withers; remnant may be present
	Ovary	Ovary wall	Pericarp	Exocarp, Mesocarp, Endocarp
		Placenta		Variously modified
		Ovule (seed)	Funiculus	Seed stalk
			Raphe	Raphe
			Micropyle	Micropyle
			Nucellus	Perisperm (seldom present)
			Embryo sac	Egg nucleus (fertilized). Embryo
				Polar nuclei (fertilized). Endosperm

THE STRUCTURE OF THE SEED

Seeds of different plants vary greatly as to size, form, external color and markings, internal structure, and amount and nature of stored food, but most seeds consist of the following parts:

Seed coat or coats.
Remains of nucellus.
Endosperm—sometimes lacking.
Embryo
- Plumule.
- Cotyledons (sometimes only one).
- Hypocotyl.
- Radicle.

The Seed Coats.—The seed coats are developed from the integument or integuments of the ovule. When two seed coats are present, the inner one (the **tegmen**) is usually thin and delicate, and the other one (the **testa**) is thick and tough. The outer seed coat is a very effective protective structure. The principal external features of mature seeds are the **hilum, raphe,** and **micropyle.** The **hilum** is a scar which marks the place where the seed broke from the stalk (**funiculus**). It is always present, but is often small and indistinct. In those plants in which the ovules become curved in development, so that the micropyle lies close to the hilum, there may be a ridge composed chiefly of a bundle of vascular elements. This ridge, formed by the stalk of the ovule and only present in anatropous ovules, is called the **raphe.**

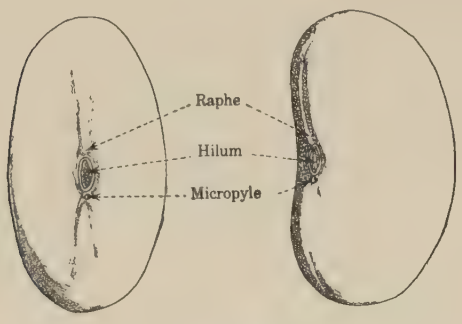


Fig. 212.

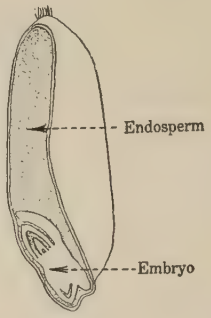


Fig. 213.

Fig. 212.—The seed of a common bean (*Phaseolus vulgaris*) showing two external views.

Fig. 213.—The fruit (grain) of wheat (*Triticum*) in longitudinal section.

The Endosperm.—In seeds which when mature are without endosperm, the endosperm has been used up by the developing embryo before the seed became fully developed. In seeds of this type, such as the common bean, pea, alfalfa, clover, etc., the stored food is in the embryo itself, mostly in the cotyledons. Conspicuous examples of seeds with endosperm are castor-oil seed, corn, wheat, and other cereals.

The Embryo.—The rudimentary plant or embryo differs very greatly in appearance in different seeds, due generally to differences in the form and relative development of the parts of the embryo, for with few exceptions all embryos are made up of the same organs.

The organs of the embryo in most seeds are (Figs. 52 and 217):

1. The plumule—a rudimentary stem, generally termed a bud.
2. The cotyledon—(or cotyledons)—seed leaves.

3. The hypocotyl—portion from the attachment of the cotyledons to the upper end of the rudimentary root.

4. The radicle—rudimentary root.

In a few plants, such as most orchids, the embryo is very rudimentary and consists merely of a small mass of undifferentiated cells. In such cases the ripening of the seed interrupts the development of the embryo much earlier than is the case in most plants. In such very rudimentary embryos, development is resumed at the time of germination, and the embryo passes through developmental stages corresponding to those through which the embryos of typical seeds pass before the maturity of the seeds.

The plumule, hypocotyl, and radicle together form the axis of the embryo. At germination the plumule develops into the shoot and the radicle gives rise to the primary root. The cotyledons are temporary leaves attached laterally to the axis of the embryo. They are unlike typical foliage leaves because of their adaption to the function of food storage or of food absorption from the endosperm. In some cases they may carry on photosynthesis for a time. The portion of the main axis of the embryo below the cotyledon and above the radicle is called the hypocotyl. It is often difficult to determine, without studying cross sections of the embryo microscopically, just where the radicle and the hypocotyl join. It is in the hypocotyl that the transition takes place from the arrangement of phloem and xylem which is characteristic of the stem to that found in young roots, that is, from the arrangement in the stem in which the phloem lies outside of the xylem to the alternating radial arrangement characteristic of young roots. At the extreme tip of the radicle there is a growing point provided with a root cap, such as is found in all typical roots. Sometimes the plumule consists merely of the stem growing point, but in many seeds the growing point of the plumule has already given rise to a number of rudimentary foliage leaves, which surround it, and thus form with the growing point a terminal bud.

KINDS OF FOOD STORED IN SEEDS

The principal kinds of foods stored in seeds are as follows:

1. Carbohydrates, chiefly
   - (*a*) Starch.
   - (*b*) Hemi-celluloses.
   - (*c*) Sugars.
2. Fats.
3. Proteins.

Starch.—This is the commonest form of food stored in seeds. It may occur either in the embryo or in the endosperm. For example, in the seeds of legumes and in many other seeds lacking endosperm the cotyledons are rich in starch; and in the cereals and other grasses, which have seeds with endosperm, starch is almost entirely restricted to the endosperm. It is formed in the cells of the developing seed by the leucoplasts from the sugar conducted to the seeds from other parts of the plant. The form of the starch grains produced by the leucoplasts is not the same in all plants. Different forms of starch grains are shown in Fig. 214. The characteristic forms and markings of the starch grains from different plants is a valuable aid in the recognition of certain adulterations in foods.

Fig. 214.—Starch grains from different sources. 1, *Diffenbachia* (After Meyer); 2, *Triticum sativum*; 3, *Phaseolus lunatus;* 4, *Phaius;* 5, *Canna;* 6, *Solanum tuberosum;* 7, *Zea mays* (1–7, after Reichert.)

The starch content of seeds varies greatly. For example, the starch content based upon dry weight, of almond seeds is 8 per cent, of navy beans, 45 per cent and of rice 68 per cent.

Hemi-celluloses.—The hemi-celluloses are complex reserve carbohydrates, largely making up the thickened walls of the endosperm of certain seeds. They are actually very different from true cellulose, being more easily rendered soluble (digested) and so more available as reserve food for the developing embryo at germination. Examples of seeds containing large quantities of hemi-celluloses are those of the date (*Phoenix dactylifera*), onion (*Allium*), *Asparagus* (Fig. 215), coffee (*Coffea*), and vegetable ivory palm (*Phytelephas macrocarpa*). The hard endosperm of the last-named plant is used commercially for the manufacture of buttons, umbrella handles, and other objects. So thick is the layer of hemi-cellulose which may be deposited on the inner surface of the endosperm walls in these plants that the lumina of the cells

may be almost closed. However, such walls are usually characterized by the presence of deep pits which penetrate the thickened part of the walls, leaving the original walls as a cross membrane. These canals permit passage of materials from cell to cell and thus make it possible for the protoplasts to remain alive for a long time.

Fats.—Fats are of general occurrence in plants, both in vegetative and in reproductive organs, but they are most abundant in seeds, where they constitute an important reserve food. Fats occur in the protoplast

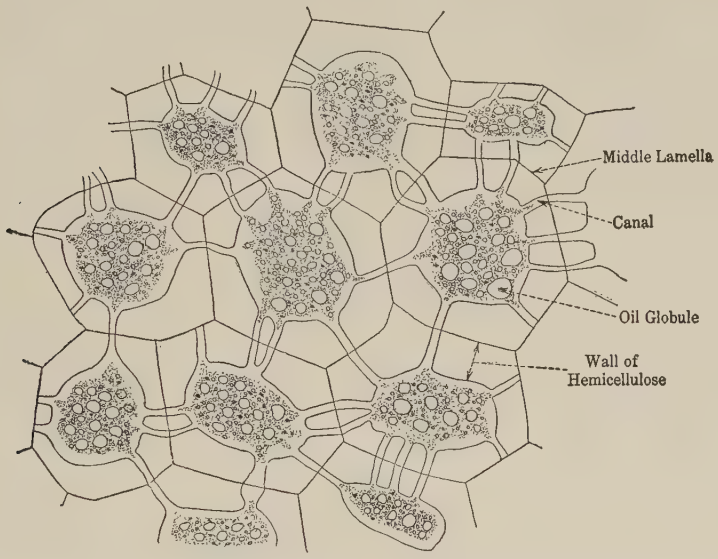


FIG. 215.—Cells from the endosperm of a common asparagus seed (*Asparagus officinalis*).

of the cells, almost always in the form of globules. Fat is usually more abundant in the embryo than in the endosperm, but in many seeds large quantities also occur as a reserve in the endosperm. A number of seeds rich in fat are cited in the following table, which also gives the commercial name of the fats and the average percentage which occurs in the seeds.

Proteins.—As already pointed out (see page 45) the proteins are organic compounds which contain oxygen, hydrogen, carbon, nitrogen and generally sulphur. Some of them also contain phosphorus. The proteins are, next to water, the most abundant constituent of the protoplasm. They are, therefore, essential for the production of new protoplasm at the growing points of the seedling shoot and root. Stored proteins are found in all seeds. They may be found occurring

as solid granules in many seeds. The members of the bean family (*Leguminosae*) store protein in their seeds in much larger quantities, relative to other forms of stored food, than do the plants of most other families.

PER CENT OF OIL IN SOME COMMON SEEDS.

Plant.	Commercial Name of Oil.	Per Cent.
Flax (*Linum usitatissimum*)	Linseed	30–39
Castor oil plant (*Ricinus communis*)	Castor	50–65
Cotton (*Gossypium*)	Cotton-seed	17–25
Coconut (*Cocos nucifera*)	Coconut	30–40
Rape (*Brassica rapa*)	Rape	33–40
Hemp (*Cannabis sativa*)	Hemp	30–35
Peanut (*Arachis hypogoea*)	Peanut	38–50 (shelled nuts)

COMMON TYPES OF SEED

Thus far, we have discussed the principal structural characters of seeds in general. We shall now give, in somewhat more detail, the structure of three representative types of seeds, namely (1) dicotyledonous type, without endosperm, (2) dicotyledonous type with endosperm, and (3) a monocotyledonous type with endosperm.

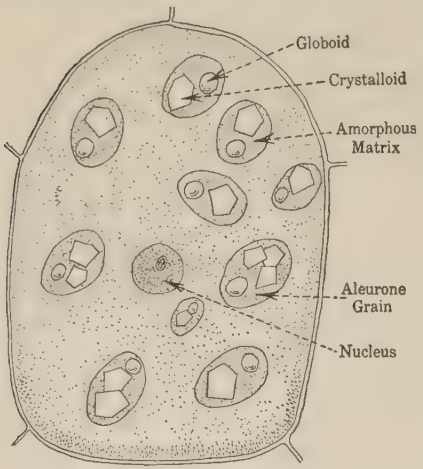


FIG. 216.—A food-storage cell from the endosperm of the seed of the castor oil plant (*Ricinus communis*).

Common Bean.—*Dicotyledonous Seed without Endosperm.*—(Fig. 212). When seeds are harvested they are broken loose from the placenta of the fruit (pod). A large oval scar near the middle of one edge, called the **hilum,** marks the place where the seed broke from the stalk. At one edge of the hilum is a small opening, the **micropyle,** present also, it will be recalled, in the ovule. The micropyle is more easily seen if the seed is soaked in water.

The position of the radicle is indicated by an elevation of the seed coat which is adjacent to the micropyle. At the edge of the hilum opposite the micropyle is a ridge which represents that part of the funiculus which is fused with the integuments. This is the raphe.

The seed coats of the bean may be easily removed from seeds which have been soaked in water. When the seed coats have been removed, the embryo of the seed is seen. This embryo consists of the following parts: (1) two cotyledons or seed leaves, (2) the young foliage leaves, between which is the first bud, all composing the embryo shoot (plumule), (3) the hypocotyl, terminating in the (4) rudimentary root or

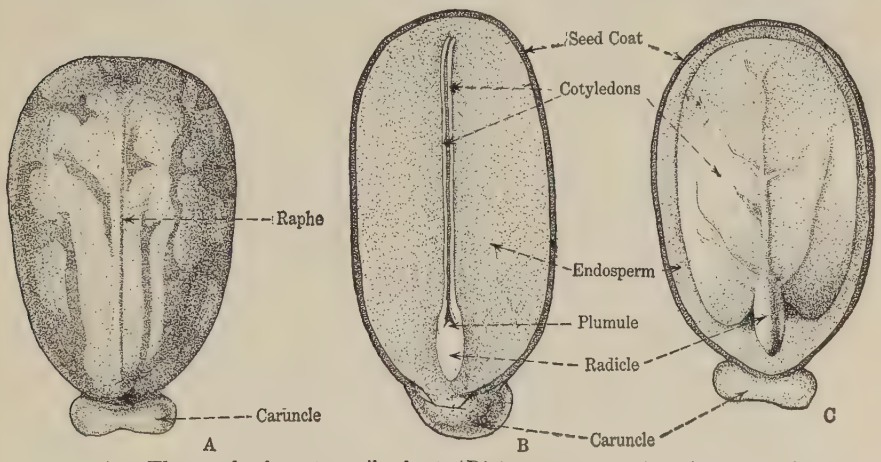


FIG. 217.—The seed of castor oil plant (*Ricinus communis*). *A*, external view. *B*, median longitudinal section cut at right angles to the broad surface of the cotyledons. *C*, median longitudinal section, cut parallel with the broad surface of the cotyledons.

radicle. The two cotyledons are large and fleshy and contain stored food, chiefly starch. Although the leaves are small, the veins within them can be easily seen.

The endosperm is lacking in the mature bean seed, having been absorbed by the developing embryo. In seeds of this type the cotyledons are the storage organs.

Castor Oil Plant.—*Dicotyledonous Seed with Endosperm.*—At one end of the castor oil seed is a spongy structure, the **caruncle,** which is an outgrowth of the testa. It covers and obscures the **micropyle.** Adjacent to the caruncle is the **hilum,** and running approximately the full length of the seed is the **raphe.** Sections of the seed show the embryo embedded in a massive endosperm.

The embryo of castor oil seed consists of two flat cotyledons, a

very short hypocotyl, a diminutive plumule, and a short radicle. The relatively slight development of the plumule and radicle in the castor oil seed is characteristic of many dicotyledonous seeds having endosperm. In dicotyledonous seeds in which the endosperm is used up by the embryo before the seed ripens, the plumule and radicle are generally (as in the bean) larger and more differentiated.

The Grass Seed.—*Monocotyledonous Seed with Endosperm.*—The grains (fruits) of cereals are of such great economic importance that it will be worth while to give a rather detailed discussion of a typical one, (wheat).

In the mature grain there is a tuft of hairs, the **brush,** at the small (stigmatic) end of the grain. Along the side of the grain, facing the

FIG. 218.—Cross section of a portion of a mature wheat fruit (grain). (After Robbins, from *Botany of Crop Plants.*)

palet, is a groove or furrow. The position of the embryo may be easily made out at the base of the grain.

In a cross section of a mature wheat grain, cut at right angles to its length, so as not to include any part of the embryo, the following layers may be recognized (Fig. 218).

1. Ovary wall or pericarp, of several cell layers.
2. Seed coat, two layers of inner integument cells.
3. Nucellus, one layer of cells.
4. Aleurone layer, outermost layer of endosperm.
5. Starchy endosperm.

The pericarp of the mature grain is composed of several layers of much compressed cells, the original cavities of which can scarcely be distinguished. The walls are thickened, cuticularized and lignified.

In the young wheat grain, the seed coat is composed of two integuments of two layers each. In the ripening process, the outer integument is entirely absorbed, so that in the mature grain the seed coat consists of two rows of cells, belonging to the inner integument. The walls of these cells are slightly lignified. The coloring matter of the grain is found in the inner layer of the seed coat. The epidermis of the nucellus which surrounds the aleurone layer is the only portion of the nucellar tissue which is present in the grain. The endosperm consists of two portions, (1) the aleurone layer and (2) the starchy or floury endosperm.

The aleurone layer is a single layer of large cells immediately within the nucellus. These cells are generally packed with aleurone grains, which are small protein bodies. This layer is often erroneously called the gluten layer. The term " gluten " is properly applied only to the principal protein found in the starchy endosperm, and should not be used in connection with the aleurone layer.

The starchy endosperm is made up of large, somewhat elongated, thin-walled cells. They are filled for the most part with starch grains. Granules of protein including gluten occur among the starch grains. Most, if not all, of the wheat starch and all of the gluten occur in this part of the endosperm.

The structure of the embryo of the wheat grain is shown in a drawing of a median lengthwise section (Fig. 52). The radicle is surrounded by the root sheath or **coleorhiza.** Between the radicle and the point of attachment of the cotyledon is the very short hypocotyl. The stem-growing point is surrounded by several rudimentary foliage leaves. The growing point and foliage leaves (together forming the plumule) are surrounded by a leaf sheath, the **coleoptile.**

In wheat, as in all members of the grass family, there is a single cotyledon. It is a structure which lies in contact with the endosperm and is specialized to absorb food from the endosperm and turn it over to the growing parts of the embryo; accordingly it remains within the seed during germination. This cotyledon, which never develops, as do the cotyledons of the castor oil seed and some beans, into a green leaf-like structure, is called the **scutellum.** On the opposite side of the hypocotyl from the scutellum is a small projection called the **epiblast.** It has been suggested that this latter structure represents a suppressed second cotyledon.

The surface of the scutellum where it adjoins the endosperm is made of a layer of cells—the columnar epithelium—which probably secretes the enzymes by which the starches and proteins in the endosperm are digested (rendered soluble). In the soluble form, these foods are able to pass from cell to cell to the growing points of the embryo.

The embryo is rich in fat or oil, mineral matter and protein, and contains considerable quantities of soluble carbohydrates, but little or no starch. About one-sixth of the embryo is fat and one-third protein, the two constituting about one-half of its dry weight.

DISSEMINATION OF SEEDS AND FRUITS

The migration of plants over the surface of the earth is accomplished in many different ways. We have seen that some plants, such as strawberries, Canada thistle, and others, migrate by means of runners, or rhizomes; this method is very slow. In others, such as the tumbleweeds (Russian thistle, witch grass, tumbling pigweed, and others), the whole plant is carried by the wind, rolling for many miles over treeless areas, scattering seed as it travels. In most plants the seeds or fruits alone are the chief means of plant migration.

There are many structural modifications by which dissemination (wide distribution from the place of their origin), of seeds and fruits is secured. Some of these adapt the seed or fruit for dispersal by wind, others for dispersal by water, and others for dispersal by animals. **Wind, water** and **animals,** including man, are the chief agencies in seed and fruit dissemination.

The following outline gives the chief adaptations favoring dispersal by various agencies and cites examples of each kind of adaptation:

1. **Adaptations Favoring Dispersal by Wind.**—

(*a*) Winged seeds and fruits. Examples: Fruits of maple (*Acer*), ash (*Fraxinus*), and elm (*Ulmus*), and the seeds of pines (*Pinus*), *Catalpa* and firs (*Abies*).

(*b*) Seeds with long, silky hairs which are epidermal outgrowths. Examples: Cotton (*Gossypium*), milkweed (*Asclepias*), willow (*Salix*), and cottonwood (*Populus*).

(*c*) Fruits with parachute-like tufts of hairs. Examples: Dandelion (*Taraxacum*), lettuce (*Lactuca*) and oyster plant (*Tragopogon*).

(*d*) Fruits with long, plumed styles which are persistent. Examples: Wind flower (*Pulsatilla*), and *Clematis.*

(*e*) Fruits with membranous envelope containing air. Examples: Ground cherry (*Physalis*), and hop hornbeam (*Ostrya*).

2. **Adaptations Favoring Dispersal by Water.**—

(*a*) Fruits with membranous envelope containing air. Example: Sedges (*Carex*).

(*b*) Fruits with coarse, loose, fibrous exocarp, as in the coconut (*Cocos nucifera*). In the irrigated districts, irrigation water is a most important factor in the dissemination of weed seeds.

Ditch banks everywhere are densely overgrown with weeds, which may shed their seeds in the water. These seeds are carried by the stream, given a good soaking in transit, and planted on a well-soaked soil—all conditions being ideal for germination. It has been found

FIG. 219.—Various seeds and fruits showing devices for dissemination. *A*, winged fruit of maple (*Acer*). B, winged fruit of ash (*Fraxinus*). *C*, winged fruit of elm (*Ulmus*). *D*, winged seed of pine (*Pinus*). *E*, barbed seed of Spanish needles (*Bidens*). *F*, milkweed (*Asclepias*) seed with tuft of hair. *G*, hairy seed of cottonwood (*Populus*). *H*, fruit of dandelion (*Taraxacum*) with parachute-like tuft of hairs. *I*, hooked fruit of cockle-bur (*Xanthium*). *J*, fruit of *Clematis* with long plume-like style. *K*, fruit of ground cherry (*Physalis*), with membranous envelope. *L*, bearded fruit of porcupine grass (*Stipa*).

that a great variety of seeds will float even though lacking special adaptations to insure buoyancy. Among such seeds are those of pig-

weed (*Amaranthus*), lamb's quarters (*Chenopodium album*), tall marsh elder (*Iva xanthifolia*), curled dock (*Rumex*), and dandelion (*Taraxacum*).

3. **Adaptations Favoring Dispersal by Animals.**—

(*a*) Fruits with beards or awns which adhere to the hair of animals, or to the clothing of man. Examples: Chiefly grasses, including porcupine grass (*Stipa*), wild barley (*Hordeum*).

(*b*) Fruits with spines. Examples: Ground bur-nut (*Tribulus*), and sandbur (*Cenchrus*).

(*c*) Fruits and seeds with hooks or barbs. Examples: Spanish needles (*Bidens*), cockle-bur (*Xanthium*) and bed straw (*Galium*).

(*d*) Fleshy, edible fruits which are eaten by birds and carried varying distances by them, and the seeds of which are then regurgitated or discharged with the excrement. Some seeds are resistant to the digestive fluids.

(*e*) Nuts which are carried away and hidden by animals, chiefly squirrels. Here are included hickory nuts (*Hicoria*), walnuts (*Juglans*), etc.

Fig. 220.—The squirting cucumber, *Ecballium elaterium*. (From Bocquillon.)

(*f*) Fruits and seeds covered with viscid material. Examples: Fruits of Sage (*Salvia*), and seeds of garden cress (*Lepidium*) and mistletoe (*Viscum*).

4. Explosive Fruits.—In a considerable number of species the seeds are scattered to some distance from the plant by the sudden and forcible rupture of the fruit. Among the most familiar examples are touch-me-not (*Impatiens*), castor oil plant (*Ricinus*) and the squirting cucumber (*Ecballium*) (Fig. 220).

Seeds and Fruits Distributed by Man.—Man in his various industrial pursuits is a most important agent in the dissemination of fruits and seeds. Probably no other means of introducing weeds, for example, is so effective as the sale and distribution of farm and garden seed, containing the seeds of various weeds. Many European plants are now at home in this country, their seeds having been brought here as "impurities," in shipments of commercial seed. Weed seeds are also carried in

screenings, in baled hay, in the packing about trees, in feedstuffs, and in manure.

SEED GERMINATION

As we have already learned, a seed is essentially a young plant (embryo) arrested in its development. It will be recalled that an individual plant does not begin its life as a seed, but instead as a single cell, called a **zygote.** The new individual plant comes into existence at the time of fertilization—when a sperm (male) nucleus from the pollen tube fuses with the egg (female) cell in the embryo sac of the ovule. By this fusion the zygote is formed. This single protoplast produced by the fusion of two protoplasts undergoes repeated division, and by growth and differentiation there results a young plant which, with its surrounding protecting coats and its stored food, is called the seed. After the seed has matured there is normally a period during which growth and development of the embryo are at a standstill. **Resumption of these activities is called germination.**

Conditions Necessary for Germination.—For this resumption of growth and development the following external conditions are essential: (1) a sufficient supply of water, (2) favorable temperature, and (3) a supply of oxygen. If any one of these is lacking the seed will not germinate.

Water.—Water plays a most important rôle in the germination of seeds. The significance of water in the life of the plant has already been discussed (see page 169) but it is well, at this point, to give special attention to the functions which water performs in seed germination.

(1) *Water softens the seed coats, and thus enables the embryo to break through them more easily.*

(2) *The water absorbed by embryo and endosperm causes the seed to swell and this results in the bursting of the seed coats.*

(3) *Water facilitates the entrance of oxygen into the seed.*—Dry cell walls are almost impermeable to gases, but if the walls have imbibed considerable water, gases can diffuse quite readily through them. As the walls of the cells of the seed coats and embryo take up water, an increased oxygen supply to the living cells results and more active respiration is made possible. On the same account, the carbon dioxide produced by respiration is able to diffuse outward.

(4) *Water dilutes the protoplasm and permits its various functions to go on actively.*—Since the protoplasm of the cells of the embryo and other living parts of the seed loses most of its water before the seeds are shed, its activities are almost completely suspended from that time

until germination. Protoplasm can not carry on actively any of its normal processes, digestion, respiration and assimilation, unless it contains much water.

(5) *Water makes possible the transfer of soluble food from the endosperm or cotyledons to the growing points of the embryo, where they are necessary for the building up of new protoplasm.*

Favorable Temperature.—For the seeds of any kind of plant there is a temperature, called the **minimum temperature,** below which germination will not take place. There is also a **maximum temperature** above which the seeds will not germinate and a temperature at which germination goes on most rapidly, that is, an **optimum temperature.** These cardinal temperatures vary widely in different species. The seeds of many " cold season crops" such as peas, lettuce, radish, barley, wheat and other small cereals will germinate readily at temperatures as low as 10° to 16° C. while the seeds of corn, pumpkin, cucumber, egg plant and many other " warm season crops " require a much higher temperature (about 21° to 27°) for good germination.

The following figures show the minimum, optimum, and maximum temperatures for the germination of a number of common species. It should be borne in mind, however, that different varieties of any one of these species may vary considerably as to their cardinal temperatures.

Plant.	Cardinal Temperatures for Germination. Degrees C.		
	Minimum.	Optimum.	Maximum.
Wheat (*Triticum sativum*)	5.0	29.0	42.5
Barley (*Hordeum*)	5.0	29.0	37.5
Corn (*Zea mays*)	9.4	34.0	46.2
Squash, pumpkin (*Cucurbita pepo*)	14.0	34.0	46.2
Scarlet runner bean (*Phaseolus multiflorus*)	9.4	34.0	46.2

Oxygen.—Oxygen is essential for germination, because without it respiration can not go on in the seed. Respiration is very active in germinating seeds, as it is in all tissues where growth and other cell activities are proceeding at a high rate. On that account large quantities of oxygen must be available to the seed if germination is to proceed normally.

THE GERMINATION PROCESSES

The principal processes going on in the seed during germination are:

1. Absorption of water by imbibition and osmosis
2. Digestion
3. Food transfer
4. Assimilation
5. Respiration
6. Growth

Water Absorption.—The initial process in seed germination is the absorption of water, and the consequent softening of the seed coats and swelling of the seed. The seed coats are largely made of material which readily takes up water by imbibition and, as is frequently the case, imbibition is here attended by a decrease in the mechanical strength of the imbibing material, in this case the cell wall material of the seed coats. The functions of the absorbed water have been discussed.

Digestion.—It was pointed out on page 285 that the principal foods stored in seeds are starch, hemi-cellulose, fats and proteins. In the seed, these stored foods cannot be transported from cell to cell and utilized in building up protoplasm and cell walls until they are changed into a soluble and hence diffusible form. **The process of rendering foods soluble and diffusible is termed digestion.** In this process certain digestive agents, which belong to the class of substances called **enzymes,** are required.

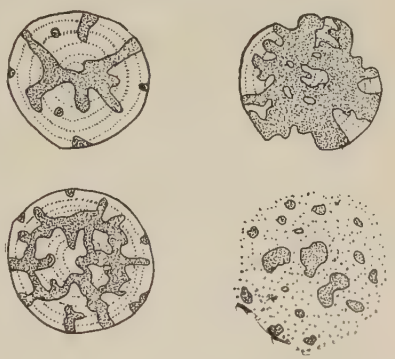


FIG. 221.—Digestion of starch grains by diastase. The four figures show successive stages of digestion. (Redrawn from Strasburger.)

Enzymes are substances, produced in living cells and probably of the nature of proteins, which resemble inorganic catalysts such as platinum in that certain chemical changes go on very rapidly in their presence but very slowly or scarcely at all when they are not present.

When fuel gas is allowed to escape into the air there is no appreciable oxidation of the gas by the oxygen of the air. If a fragment of asbestos covered with finely divided platinum is held in the mixture of gas and oxygen the oxidation of the gas will go on at a rapid rate and produce so much heat that a flame will be produced, the gas will be

lighted. Besides platinum a number of other substances not produced in living cells have a similar power of " speeding up " chemical changes without their being used up themselves during the process. Some of these inorganic catalysts are of very great utility in the chemical industry.

It is impossible to exaggerate the importance of the organic catalysts, or enzymes, which are produced in the living cells of plants and animals. They greatly accelerate the rate of many important changes in cells which otherwise would practically not go on at all. Also, due to the presence of the proper enzymes, changes may go on in living cells at relatively low temperatures (below 40° C.) which would otherwise go on at the same rate only at such high temperatures as would be fatal to all living protoplasm. No enzyme has been secured in sufficient purity to determine its exact composition. The principal characteristics of enzymes may be summarized as follows:

1. They are produced by living protoplasm.

2. They may be separated from protoplasm and still retain their activity for years if stored under proper conditions.

3. They are effective in small quantities.

4. They are sensitive to heat; heating to 60° C. permanently destroys them.

5. They are generally specific, one enzyme being effective in one chemical change only. Thus diastase changes starch to certain sugars and zymase converts glucose into alcohol and carbon dioxide, but neither is able to bring about any chemical change other than the characteristic one mentioned.

Digestion, rendering insoluble substances soluble and diffusible, is only one of a great many different kinds of changes which are brought about by enzymes.

The principal classes of digestive enzymes found in seeds and the products of the digestion which they carry on are:

Enzyme.	Substance Digested.	Soluble Products.
Amylase (diastase)	starch	maltose (a sugar)
Cytase	hemi-celluloses	mannose and galactose (sugar)
Lipase	fats	glycerine and fatty acids
Proteases	proteins	amino acids

Food Transfer.—Absorption of water, the secretion of enzymes, and digestion are but preliminary to the transfer of food from the storage cells to the growing parts of the germinating seed. Conductive tissue is poorly developed in the rudimentary plant or embryo seed. Hence, transfer of material from one part to another must be almost entirely by diffusion from one living cell to another. In the germinating seed

a diffusion gradient is established. From our discussion of diffusion in Chapter II, we understand that any substance tends to diffuse from a region where there are more dissolved particles of that substance per unit volume of solution to a region where there are fewer particles of that same substance per unit volume. At the growing points of the embryo, soluble foods are being transformed into cellulose walls and into protoplasm, and are thus being removed from solution. Hence a

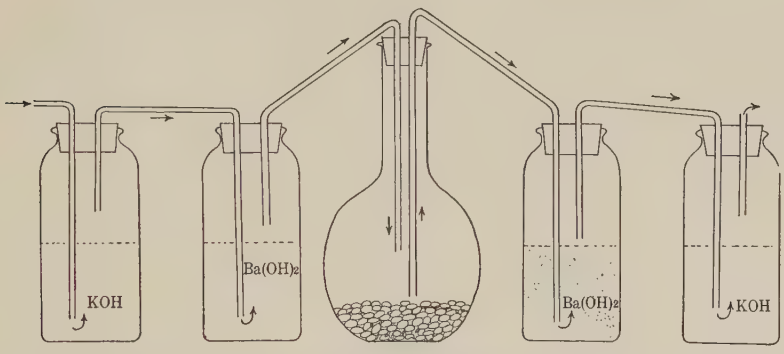


FIG. 222.—Diagram of apparatus used to demonstrate the evolution of carbon dioxide from actively respiring seeds. Air enters the apparatus by the tube at the left and passes through in the direction shown by the arrows. As the air bubbles through the solution of potassium hydroxide (KOH) in the first bottle the carbon dioxide gas in the air is absorbed by the solution, potassium carbonate being formed and remaining in the solution. The air is next passed through a solution of barium hydroxide $Ba(OH)_2$ to show whether all the carbon dioxide has been absorbed by the KOH solution. If the carbon dioxide had not been completely removed a white precipitate of barium carbonate would be formed. The absence of any such precipitate shows that the air passing into the flask containing germinating seeds is free of carbon dioxide. The evolution of carbon dioxide by the seeds is shown by the formation of the white precipitate of barium carbonate ($BaCO_3$) as the air from the flask is drawn through the next bottle. The KOH bottle at the right serves to prevent any carbon dioxide from passing in the reverse direction.

constant reduction in the concentration of soluble foods is going on at the growing points. The direction of movement of soluble foods is toward these points of relatively low concentration of such substances, and away from the parts of the seed (storage regions) where soluble foods are being produced by the action of enzymes upon the insoluble stored food.

Assimilation.—This is the final step in the utilization of the stored food. It is the transformation of the digested foods into the living

substances (protoplasm) and of certain of these foods by the protoplasm into cell walls. This change from dead to living matter may be said to be the most important, as it is also the most interesting, change which takes place in organisms. We know almost nothing about the process, however, for an understanding of it would necessitate our first learning much more than is now known of the actual nature of protoplasm.

Respiration.—Respiration goes on more actively in germinating seeds than in almost any organ or tissue of the autophytic plants. It will be recalled that respiration is an energy-releasing process in which part of the food is broken down into very much simpler compounds, such as carbon dioxide and water, and the energy stored in the food is released. This released energy is in part used by the seedling plant in the work of building up the complex compounds of which the plant is composed. Much of it, however, is dissipated as heat.

Consideration of the equation for the respiration of glucose, $C_6H_{12}O_6 + 6O_2 = 6CO_2 + 6H_2O$, would lead us to expect that respiration would be accompanied by a loss of weight, if no other process went on at the same time which added to the weight. If seeds are germinated in distilled water and in the absence of light, water absorption would be the only process which could increase their weight. It is possible therefore by comparing the dry weight of the two lots of seeds (originally of the same weight) one lot of which has remained ungerminated while the others have grown into seedlings under the conditions mentioned above. to demonstrate that respiration causes loss of material from the plant. Under the conditions of such an experiment no photosynthesis or intake of mineral salts could take place. The loss in dry weight is due to respiration. The following table (from Palladin) shows this loss of dry weight in the case of a number of seeds.

Plant.	Total Dry Weight in Grams,		Loss in Dry Weight During Germination, in Grams.
	Seed.	Seedling.	
Wheat (*Triticum sativum*) Analyses of 46 seeds	1.665	0.722	0.943
Corn (*Zea mays*) Analyses of 22 seeds and seedlings	8.636	4.529	4.107
Lupine (*Lupinus luteus*)	100.00	81.70	18.30
Sunflower (*Helianthus*)	100.00	88.98	11.12

That germinating seeds respire very actively is shown by the large quantity of carbon dioxide which they give off. Germinating lettuce seeds may produce as much as 82 cc. of carbon dioxide per gram of dry weight in twenty-four hours at 16° C. and poppy seeds as much as

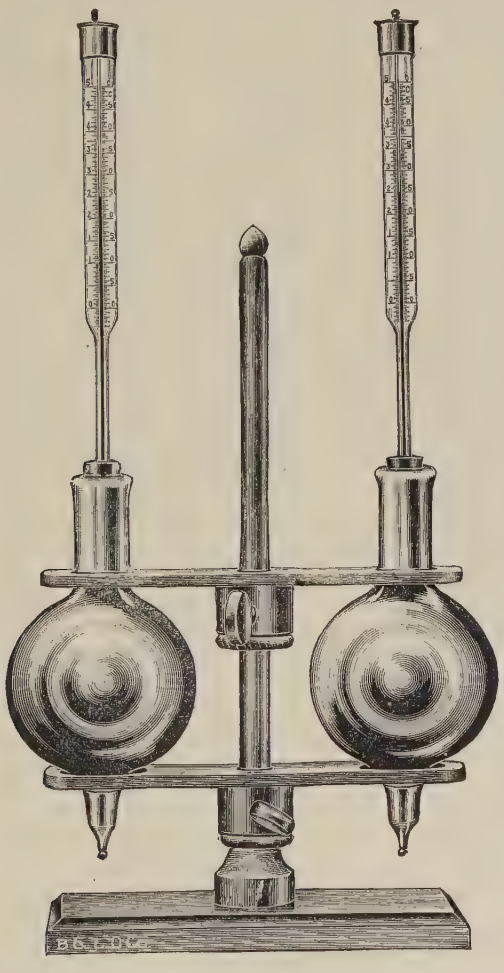


Fig. 223.—Apparatus for demonstrating that heat is liberated during the respiration of germinating seeds. The two receptacles used are Dewar flasks which are similar in construction to "thermos" bottles and which greatly reduce heat loss and absorption of heat from without. Two lots of seeds of equal weight and of the same kind are used in the experiment. Both lots are so treated that the bacteria and fungus spores on the surface of the seeds are killed. Then one lot is killed by boiling or other treatment and after both lots have acquired the same temperature they are placed in the two flasks and the stoppers with thermometers inserted. After a few hours the living seeds will be found to be several degrees warmer than at the beginning of the experiment while the temperature of the dead seeds will be unchanged. (Cut loaned by the Bausch & Lomb Optical Company.)

122 cc. per gram in the same time and at the same temperature. Fig. 222 illustrates an experiment to demonstrate carbon dioxide evolution during the germination of seeds. Similar apparatus might be used to measure the quantity produced.

Part of the energy liberated in respiring seeds is in the form of heat. Fig. 223 shows an apparatus for demonstrating this heat liberation which is also evident from the fact that a mass of germinating barley

or other seeds when germinating may, if rapid loss of heat is prevented, actually feel warm to the hand. The very active respiration of seeds in germinating is necessary in order that the large quantity of energy for the activities of the embryo may be supplied.

Growth.—The swelling of the seed, due to imbibition of water and to growth, is followed by the bursting of the seed coats. Freed from the seed coats, supplied with water and dissolved foods and with oxygen for respiration, the embryo now grows actively. Its growth is due (1) to the enlargement of cells already formed (largely by the absorption of water into the vacuoles, and the stretching of the walls) in the embryo and (2) to the production of new cells at the growing point of the radicle and the plumule. The growth of the radicle and the plumule into root system and shoot system correspond in all particulars with the development and differentiation of tissue from the growing points of the root and terminal bud as described earlier in this book.

FIG. 224.—Stages in the germination of wheat. *c*, coleorhiza; *g*, coleoptile; *r*, roots,; *s*, embryo. (After Bocquillon.)

The radicle is usually the first embryo structure to protrude from the seed. It grows downward, sends out branches, develops root hairs and thus enlarges its absorbing surface.

In many plants, such as the common bean, sunflower, and squash, the cotyledons and plumule are brought up to the light by the growth of the hypocotyl, the seed coats generally remaining in the soil. In oaks and in other plants, such as garden pea and scarlet runner bean, the cotyledons remain below the ground. In the cereals, the one cotyledon (scutellum) does not come to the surface. After the young plant reaches the light and develops chlorophyll-bearing tissue, it is no longer completely dependent upon the store of reserve food within the seed, but is now able to carry on photosynthesis.

CONDITIONS AFFECTING THE VITALITY OF SEEDS

By the vitality of seed is meant its capacity to germinate and produce seedlings capable of developing into an adult plant. Among the chief factors which determine the vitality of seeds are the following: (1) Vigor of the parent plant, (2) conditions to which the seeds are exposed while developing, (3) maturity of the seeds, (4) conditions under which the seeds are stored, (5) age of the seeds.

(1) **Vigor of the Parent Plant.**—Weakly parent plants often produce seeds which are deficient in stored food material and the embryos of which are abnormally small. The plants grown from such seeds are often less vigorous than those produced from normal seeds.

(2) **Conditions to which the Seeds are Exposed while Developing.**—The amount of moisture in the atmosphere and its temperature during the period of seed maturing may influence the vitality of the seeds. Most seeds mature best under dry atmospheric conditions. Low temperatures early in the autumn may injure the partly mature seed. Corn, for example, suffers from freezing if the grain is not thoroughly dry. Corn containing 13 per cent moisture, however, may be stored with safety in bins exposed to temperatures much below freezing.

(3) **Maturity of Seeds.**—Although seeds will often germinate before they have reached full maturity, the plants grown from such seeds are usually weak, as is evidenced by the fact that they can not withstand such unfavorable conditions as can those from fully matured seeds. Moreover, the yield from immature seeds is lower than from properly matured seeds. Immature seeds lose their vitality much more quickly than do mature seeds.

(4) **Conditions under which Seeds are Stored.**—In a ripe seed, the essential part of the seed, the living embryo, is in a relatively inactive state. The conditions under which seeds are stored should be such as to keep the embryo in this inactive state. That is to say, the temperature should be kept fairly low and uniform, and the atmospheric humidity relatively low. If seeds are not stored in a dry place, the moisture present may be sufficient, provided there is the proper temperature and oxygen supply, to start germination. If germination processes are started, it follows that the respiration rate increases, tnat there is a loss of dry weight, and a consequent decrease in the amount of stored food and therefore of stored energy in the seeds. Seeds stored in bulk, under such conditions may " heat." This may be due in part to heat liberated by the respiration of the seeds themselves and in part to the heat of respiration of fungi and bacteria growing on the seeds. The heat thus developed may become so intense as to actually kill the embryos.

(5) **Age of Seeds.**—All seeds gradually lose their vitality with the lapse of time. The rate at which they lose their vitality depends upon the kind of seed and upon the condition of storage. The seeds of willow (*Salix*) for example, die unless they germinate within a few days after they are shed. On the other hand, the seeds of some legumes have been known to retain their vitality for from fifty to eighty years. Ewart found that if the decrease in the percentage of germination which he observed in certain seeds over shorter periods continued at the same rate, some of the seeds which he used would retain their vitality for 150 to 200 years. Recent studies of Indian lotus (*Nelumbo nucifera*) fruits which had lain buried in a peat bed probably for over 200 years showed a very large percentage of the seeds to be still capable of germination. However, there is no reason for believing any of the frequent reports that the seeds placed in Egyptian tombs thousands of years ago are still capable of germination.

Seed Testing.—Although there is often a correlation between size or weight of seed and its vitality, it is impossible to distinguish living from dead seeds without conducting actual germination tests.

It is the practice of many growers to determine the percentage of germination of seed intended for planting. This is done by taking several hundred of the seeds and placing them in moist soil, sand, or sawdust, or between folds of cloth or blotting paper, and keeping them at a proper temperature. After a period, the length of which will depend upon the kind of seed, a count may be made of the seeds which have germinated and the percentage of viable seeds may be determined.

DORMANCY OF SEEDS

Many seeds, though viable, are incapable of germination immediately after they become mature. This characteristic of certain seeds is called **dormancy** or **delayed germination.**

Causes of Seed Dormancy.—Delayed germination in seeds may be due to several causes.

(1) *Rudimentary embryos.*—Some seeds, such as those of *Gingko*, buttercup (*Ranunculus ficaria*), corydalis (*Corydalis cava*), herb-Paris (*Paris quadrifolia*), and others, have immature embryos at ripening time. They must complete their development before germination, and the process of maturing may require weeks and sometimes months under favorable conditions.

(2) *Seed Coats which Prevent the Intake of Water.*—The so-called "hard seeds" of alfalfa, sweet clover, and other legumes often fail to grow readily even when placed under excellent conditions for germina-

tion because their seed coats are highly impermeable to water. The permeability of their seed coats can be increased by " scarifying," that is, by scratching the surface by various means. As a result, water can enter the seed more readily and germination soon takes place. Otherwise it may be years before sufficient water enters to make germination possible.

(3) *Embryos Incapable of Rupturing the Seed Coats.*—In this case the embryos are mature and seed coats do not inhibit the intake of water but the pressure of the growing embryo is not sufficient to break the seed coats. Common pigweed (*Amaranthus*) seeds fall in this class. The exposure of such seeds to freezing and thawing and to the action of soil organisms gradually softens the coats and makes germination possible.

(4) *Retardation of Gaseous Exchange.*—The tissues surrounding the embryo may prevent the ready intake of oxygen by the embryo and perhaps also the giving off of carbon dioxide. This inhibition of gaseous exchange not infrequently retards or prevents the growth of the embryo. The seeds of cocklebur (*Xanthium*) are delayed in germination on this account.

(5) *After-ripening.*—The embryos of some seeds, such as those of hawthorn (*Crataegus*), appear to be incapable of germination even when the seed coats are removed and all external conditions are favorable for germination. Experiments show that the delay is not due to any of the four causes already mentioned. Such seeds must go through a series of changes known as " after-ripening." In the hawthorn it has been found that the principal change associated with after-ripening is an increase in the acidity of the cell sap in certain portions of the embryo. It is believed that this acidity produces conditions which favor the absorption of water and the formation and activity of enzymes, and thus stimulates growth. In the hawthorn, the after-ripening process may be hastened by treating the seeds with dilute acids. This process may also be hastened in some instances by exposure of the seeds to low temperatures, particularly to freezing or to successive freezing and thawing.

SEEDLINGS

From the time when the young plant emerges from the seed to the time when it becomes entirely dependent upon food manufactured by itself, it is called a seedling. Seedlings may be divided into two quite distinct types, as follows:

1. Those in which the cotyledon or cotyledons are raised above the ground, where they may function for a time as photosynthetic organs

The elevation of the cotyledon or cotyledons is brought about by the lengthening of the hypocotyl.

2. Those in which the cotyledon or cotyledons remain beneath the ground. In this type of seedling, the hypocotyl undergoes little or no elongation.

The first type of seedling is illustrated by the onion (*Allium*) among monocotyledons, and among dicotyledons by such well-known plants as the common bean (*Phaseolus vulgaris*), squash (*Cucurbita*), sunflower (*Helianthus*), and apple (*Malus*).

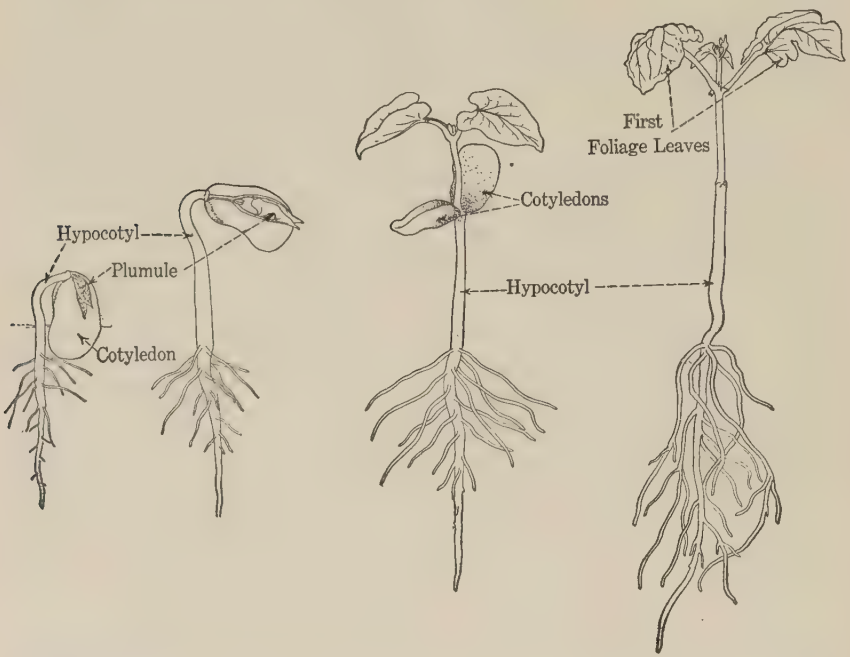


FIG. 225.—Stages in the germination of the seed of common bean (*Phaseolus vulgaris.*)

The second type of seedling occurs in all grasses and in many other monocotyledons, and in such dicotyledons as peas (*Pisum*) and scarlet runner bean (*Phaseolus multiflorus*).

Several stages in the germination of the common kidney bean (*Phaseolus vulgaris*) are shown in Fig. 225. Note that the two cotyledons are brought above ground through elongation of the hypocotyl. Though some of the stored food in the cotyledons has been used by the developing root, a considerable quantity still remains. Even before this is exhausted the cotyledons, which are now in the light, become green and carry on photosynthesis to some extent. However, the reserve

food in them is gradually used up by the developing plant, and they shrivel until finally their epidermis alone remains. As soon as the cotyledons unfold, the plumule begins to grow more actively, and very soon true foliage leaves are exposed to the light and begin their functions of carbohydrate synthesis and transpiration.

In some plants, such as the castor oil plant and buckwheat, the cotyledons are thin, and contain little stored food. They absorb food

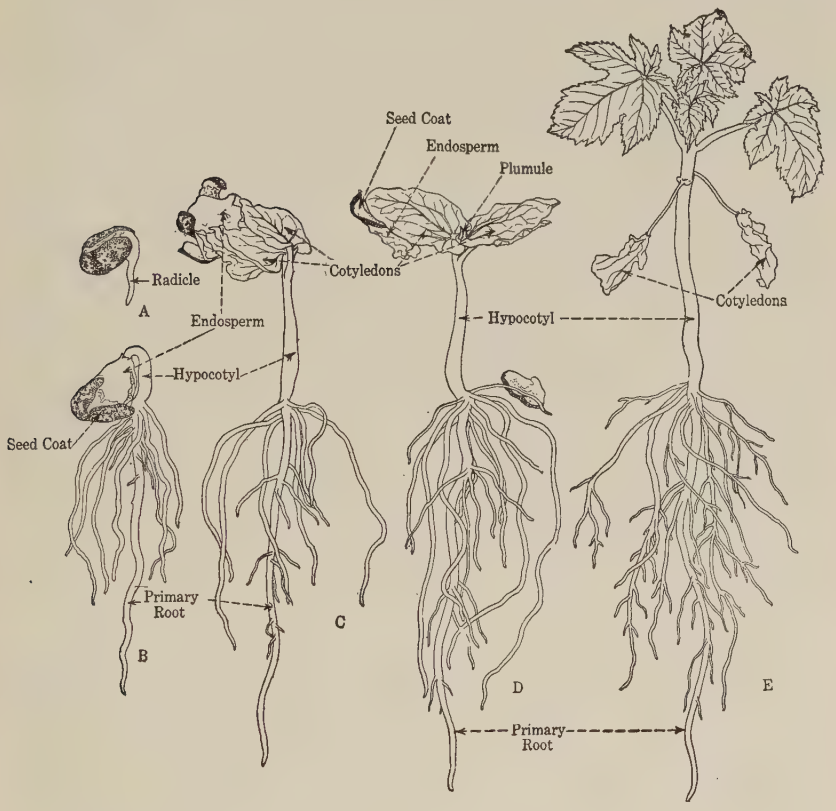


FIG. 226.—Stages in the germination of a seed of castor-oil plant (*Ricinus communis*).

for the embryo from the endosperm and later serve temporarily as photosynthetic organs. They remain attached to the seedling much longer than in common beans and carry on active photosynthesis.

In the onion the primary root, soon after the beginning of germination, is forced out by the growth of the curved cotyledon of the embryo, which soon comes above the surface of the ground in the form of a closed loop. The tip of the cotyledon adheres to the endosperm and

seed coat. The endosperm and seed coat may be pulled from the ground when the soil is loose, but if it is compact they remain beneath the ground. Nourishment is absorbed from the endosperm by the cotyledon. When this is exhausted, the tip of the cotyledon shrivels and becomes separated from the seed coat. A longitudinal slit now appears at the base of the cotyledon, and through this the first foliage leaf emerges. The cotyledon later disappears altogether.

The type of germination described in the onion is found in many monocotyledons and in some dicotyledons. There are modifications, however. For example, in spiderwort (*Tradescantia*), and date palm (*Phoenix dactylifera*), the cotyledon is at first small, but enlarges as the reserve material is absorbed, and comes to occupy the space vacated by the latter. In this case the cotyledon is an absorbing structure.

In the germination of the wheat grain, the primary root is the first embryo structure to emerge. The coleorhiza is ruptured but remains as a collar about the root where it breaks through the grain coats. Very soon several lateral roots appear, which together with the radicle constitute the primary root system. The growing point of the shoot elongates, the young leaves being enclosed by the leaf sheath or coleoptile, a closed and pointed organ. The first foliage leaf enlarges and breaks open the end of the coleoptile. The point of attachment of the first foliage leaf is at the first node, which is a very short distance above the cotyledonary plate or node. It is from the first leaf node that the first permanent (adventitious) roots arise. Other whorls of permanent roots arise from the nodes above. Thus there are formed clusters of permanent roots at the basal nodes, which are separated by very short internodes.

The germination of wheat illustrates a type occurring in all grasses. In this group, as has been seen, there is one cotyledon (**scutellum**), which remains within the seed. It serves as a food-absorbing and food-transporting organ. The primary root system (seminal root system) is temporary and soon dies. It is replaced by successive whorls of permanent roots.

CHAPTER IX

RELATION OF THE PLANT TO ENVIRONMENT

In the preceding chapters of this book, reference has frequently been made to the effect of various external conditions or factors upon the development, structure, and activities of the various organs of the seed plant. It will be well to bring together here a statement of these various factors and their effects upon the plant. Collectively, these external factors are spoken of as the environment, and their effect upon plants and animals in nature is the special field of that branch of biology which is called ecology. It is well known that two individuals of a given plant species may differ very greatly if grown in different environments. Thus, most plants of a given species differ greatly in size, form, foliage, and other particulars, when grown in dry, hard soil by a roadside where they are exposed to strong sunlight, from other plants of the same species grown in a cool, moist, and shaded ravine. Trees of a given species grown near timber line are strikingly different from individuals grown at lower altitudes. It is convenient to classify the environmental factors into three groups:

1. *Climatic factors,* those which act upon the plant through the atmosphere.
2. *Edaphic factors,* those which operate through the soil.
3. *Biotic factors,* those arising from the presence of other plants and animals.

Some of the principal factors under each of these three groups are:

Climatic factors—

- Heat
- Light
- Carbon dioxide
- Atmospheric humidity and precipitation
- Wind

Edaphic factors—

- Available water in the soil
- Air in the soil
- Temperature of the soil
- Quantity and nature of the soil solutes

Biotic factors—

Competition among different species
Grazing by animals
Soil bacteria, algae, and protozoa
Parasitic fungi
Insects that injure plants
Insects that carry on pollination

HEAT

Each of the physiological processes which go on during the life of the plant has certain temperature limits (maximum and minimum) between which it can take place, and a characteristic temperature (optimum) at which it goes on most actively.

The minimum, optimum, and maximum temperatures for one process may differ considerably from those of another process taking place in the same plant at the same time. Moreover, in the case of a given process, such as photosynthesis, the cardinal temperatures may vary rather widely in different species. The minima seldom are lower than one or two degrees above 0° C., and the maxima are generally below 45°. Even in those parts of the world where the temperature for a period is below the minimum for vital activities plants may exist. In such cases the plants remain dormant except for the relatively short periods during which the temperature rises above the minimum. It is a familiar fact that some plants not only can not carry on their vital functions at low temperatures but are actually killed even by short exposure to temperatures at or slightly below the freezing point of water. It is also recognized that different tissues of the same plant vary in their resistance to low temperatures. In our common woody plants, the tissue least resistant to freezing is the pith; the next least resistant is the sap wood, then the bark, and the most resistant in well-matured and well-hardened stems, is the cambium. However, in actively growing stems, the cambium is not as resistant to freezing as other tissues.

Injury resulting from freezing temperature appears to be due, in part at least, to the rapid withdrawal of water from the cells; this is accompanied by the formation of ice crystals in the intercellular spaces.

In some of these cases the resistance to low temperatures seems to be due to peculiarities, as yet unexplained, of the protoplasm, which makes it immune to the injurious effects attending ice formation. In other cases it is undoubtedly due to certain substances, sugar, for example, which are present in the cell sap in such quantities as to prevent freezing of the water in the protoplasm except at very low tempera-

tures. At 0° C. pure water freezes, but any non-volatile solutes in solution in water lower the freezing-point. The greater the concentration of solutes in the solution the lower will be the freezing-point. The change of stored starch into sugar, which takes place at low temperatures in some plants, is a response of the plant which protects it from being killed by low temperatures. Plant parts whose protoplasm is relatively low in water content (seeds, for example) can withstand very low temperatures without injury. Often young shoots whose living tissues contain much water are killed by frost though older stems whose cell sap is more concentrated may survive. The maturing of plant tissues that takes place in late summer, autumn or early winter seems to influence the resistance to winter temperatures. Well-matured tissues are more resistant than those not completely matured.

Gardeners commonly practice the process of "hardening" their transplants. If a tomato plant, for instance, is removed suddenly from a warm greenhouse in the spring to the garden out of doors, it has little resistance to low temperatures, and the death point, temperature at which it will be killed by cold, is relatively high. The usual procedure is to move the plants from the greenhouse to a cold frame where, after remaining for a time where the temperatures are intermediate between those of the greenhouse and out of doors, the plants may be planted with safety in the open.

Differences in temperature in different parts of the world and at different altitudes constitute what is probably the most important factor in determining what plants shall or shall not grow in a given region.

LIGHT

We shall mention only a few of the effects which differences in intensity of light produce in the structure and activities of plants. By the term light we mean to include all the energy (radiant energy) which reaches the plant from the sun. Light may affect the plant and its activities in the following ways:

1. By reason of the dependence of the process of photosynthesis on the intensity of illumination.
2. By heating effect.
3. By furthering transpiration through heating of the leaf.
4. By its effect upon the direction of growth of certain plant organs and upon orientation of leaves.
5. By its effect upon distribution of plants.
6. By its effect not only of light intensity but of duration of illumina-

tion upon the rate of growth and development of plants and particularly upon flower production.

7. By its effect upon the form and internal structure (anatomy) of leaves.

8. By its effect upon the form of the shoot system of plants.

As we have already learned, the rate of growth of green plants past the seedling stage will be largely determined by the surplus of food produced above that respired. The amount of this surplus will depend, within certain limits, upon the intensity and duration of illumination. Very intense direct sunlight, however, may be detrimental to plants (1) because it may endanger the living protoplasm by raising it to very high temperatures, (2) because it may increase transpiration to a dangerous intensity, (3) because it disintegrates chlorophyll and (4) because it retards growth.

Plants growing in habitats where they are exposed much of the time to very strong sunlight generally have smaller leaves and shorter internodes than shade plants and are accordingly of more compact form. The difference between the form of trees which have developed as isolated individuals and that of others of the same species which have grown in a forest, closely surrounded and accordingly largely shaded by other trees, is due to differences in illumination. Many other examples of the effect of illumination upon the form of the shoot system could be cited if space permitted. The leaves of shade plants, in addition to being in general larger than those of sun plants, are almost always more or less horizontal so that the light falls upon them at right angles to their surface. Those of sun plants, such as eucalyptus and the various so-called compass plants (such as *Silphium laciniatum*), hang down or are held perpendicular so that the sun's rays strike the leaf surface at an acute angle and much less radiant energy is absorbed by the leaves (Fig. 153). Due to the weakness of illumination available to them, shade plants often so place their leaves (forming a leaf mosaic) (Fig. 136) that small leaves occupy the spaces between the larger leaves. Thus, shading of one leaf by another is avoided and the maximum exposure of leaf surface to the light is attained. Since the various species of sun plants and of shade plants are adapted to differences in illumination, so that they can develop best in habitats which are respectively intensely and weakly illuminated, it follows that the distribution of these plants in nature will be determined by the intensity of illumination in different locations.

One of the most striking examples of the relation between illumination and the development of certain species is furnished by the spring flowering plants of the floor of dense deciduous forests. In the early

spring before the trees have developed their leaves, the floor of such a forest is well lighted, but later, owing to the growth of foliage of the trees, little light reaches the ground. Many small plants, such as Dutchman's breeches and squirrel corn (species of *Dicentra* and *Clintonia*) growing in such locations develop their leafy shoots from persistent underground storage structures very early in the spring. These utilize the light available before they are shaded by the foliage of the tree above them, and after a period of very active food manufacture and subsequent flowering they die. In this short period of development they accumulate enough reserve food to make possible the rapid development of another crop of leafy stems early the next spring. Evidence has recently been secured which seems to indicate that in the case of many crop plants the development of flowers is dependent not so much upon the intensity of light as upon the relative length of day and night. Thus some species have been brought to unusually early flowering, and in other species flowering has been postponed, by artificially lengthening the daily period of illumination.

Differences in illumination are no doubt largely responsible for the very great differences in the internal structure of sun plants and shade plants. The following are the principal anatomical characteristics of the leaves of sun plants and shade plants:

SUN PLANTS	SHADE PLANTS
Thick palisade parenchyma, the cells being longer or the number of layers of palisade cells being greater	Thin layer of palisade cells or none at all
Spongy parenchyma not well developed	Well-developed spongy parenchyma
Thick leaves	Thin leaves
Small intercellular spaces	Large intercellular spaces
Thick and heavily cutinized epidermis	Thin and slightly cutinized epidermis
Stomata confined to lower side or more abundant or the lower side	Stomata on both sides, the number on the two sides nearly or quite the same
Frequently smooth and shiny surface, capable of reflecting much of the light falling upon them	Generally dull surfaces
Often densely hairy	Seldom very hairy.

Similar differences are frequently found between different individuals of the same species which are growing respectively in sunny and in shaded habitats.

CARBON DIOXIDE

Under natural conditions concentration of carbon dioxide in the atmosphere is very low (3 parts in 10,000) and varies only within narrow limits. Accordingly, though this factor in the environment is of immense importance, there are no recognizable effects upon plants growing naturally which can be attributed to differences in carbon dioxide supply. The solubility of gases is less at higher temperatures than at lower temperatures. Since solution is one of the steps in the absorption of carbon dioxide gas by the green cells of the leaf, no doubt the influence of temperature upon carbon dioxide absorption is one of the many factors which determine the optimum temperature for photosynthesis.

PRECIPITATION AND ATMOSPHERIC HUMIDITY

Precipitation.—The significance of water for the life of the plant and the various indispensable roles which it plays in the various vital processes have already been discussed (Chapter V, page 169-172). In this chapter we shall merely enumerate the ways in which variations in the water of the atmosphere may affect the plant. The water in the atmosphere is present as **water vapor** dissolved with the other gases. Condensation of this results in **precipitation,** that is, water in the liquid form (rain) or the solid form (snow). Precipitation is a factor second in importance only to temperature in determining the distribution of different plants in the various regions of the earth. It is not so much the total amount of rain falling throughout the year as the distribution of the rain over the whole year which determines what kind of plants will grow in a given region. For example, in the tropics where the rainfall is heavy and rather uniformly distributed throughout the year, the dominant vegetation is an evergreen forest; on the other hand, in those parts of the tropics where the total rainfall for the year is equally heavy, but occurs during a few months of the year, the forests are chiefly of the deciduous type.

Of the total precipitation, a part is absorbed by the soil, a part runs off and enters streams, and hence does not become available to plants, and a small portion is absorbed directly by such plants as certain algae, lichens, mosses, and by a few seed plants which have special aerial absorbing organs. As an example of the latter, are the aerial roots of certain orchids which are covered with a spongy layer of absorbing tissue.

Even though the total yearly rainfall is the same, the plants found in a region where the precipitation falls during very heavy storms but

within a relatively short period will be very different from those found where the rainfall is more or less uniform throughout the year or at least throughout the warmer part of the year.

Atmospheric Humidity.[1]—There is always, even in the driest regions, some water present in the air in the form of gas (water vapor). The water vapor in the atmosphere is spoken of as atmospheric humidity. When the air contains all the water vapor it can hold it is said to be saturated, but the percentage of water in a saturated atmosphere varies widely with the temperature. Air which is saturated when it is at a low temperature will be far from saturated at considerably higher temperature, for with rise in temperature its capacity for holding water vapor increases. Air saturated at a relatively high temperature loses some of its water vapor when it is cooled. When that occurs, small drops (mist or fog) or larger drops (rain) are formed but the air remains saturated at the lower temperature. Any subsequent increase in temperature results, however, in the air becoming less than saturated, unless it absorbs water meanwhile from free water surfaces. The humidity of the air surrounding the plant is the most important single factor in determining the rate of transpiration. Low humidity is often assumed to be principally responsible for the various devices which plants employ to reduce transpiration. (See discussion of transpiration, Chapter VI, pages 219–226.) It is not, however, the percentage of water vapor in the atmosphere which determines, other things being equal, how rapid transpiration shall be. It is, instead, the percentage of water which the air can still absorb before saturation is reached. With a given percentage of water in the atmosphere, this quantity increases with increase in temperature.

[1] The amount of moisture in the air may be expressed in several different ways. One of the most used and most convenient methods is to express it in terms of relative humidity. By relative humidity is meant the amount (weight) of water vapor in any quantity of air, compared with the total amount of water vapor which the air is capable of holding at the temperature in question. Thus air which is water saturated has a relative humidity of 100 per cent. If only half the amount of water vapor necessary to saturate it is present the relative humidity is 50 per cent. Thus if air is in contact with a free water surface it is able at 0° C. to absorb water until in one kilogram of this saturated air there are 3.78 grams of water vapor. If this quantity of air, now having a relative humidity of 100 per cent, was raised to 10° C., without its having opportunity for the absorption of more water, its relative humidity would be almost exactly 50 per cent because the quantity of water present in a kilogram of saturated air at 10° is 7.53 grams or almost twice 3.78 grams. In the above statement it is assumed that atmospheric pressure remains constant at 76 cm. of mercury.

WIND

One of the principal effects of wind on plants is that of increasing the rate of transpiration. In a still atmosphere, a layer or cap of moisture-laden air accumulates about the transpiring leaf surface, retarding somewhat the diffusion of water vapor outward; if, however,

FIG. 227.—"Wind timber" on the slopes of Arapahoe Peak, Colorado, at an altitude of 11,500 feet.

this vapor cap is carried away by wind as fast as it accumulates, water vapor escapes at a greater rate from the leaf. If the winds which blow over the surfaces of leaves are moisture-laden, as when they have crossed large bodies of water, and are cool, they are less effective in hastening the rate of water loss from the plant than are dry warm winds which are such as have crossed dry, hot land areas.

Aside from the indirect effects of wind upon the plant, in locations where there are strong prevailing winds the trees are generally smaller than in other localities, the trunks are frequently bent away from the wind, and branches on the windward side are often almost entirely suppressed so that the tree has a one-sided form. To what extent these results are due to the mechanical effect of the wind is not altogether clear. Certainly the deformations of the exposed trees on sea coasts and on mountain tops (Fig. 227) are largely due to strong winds, though in the latter case the weight of the winter snow accumulated on the branches is also an important factor. The main stems of trees which grow in places where they are exposed to strong prevailing winds do not grow in thickness equally on all sides. The stems have longer diameters in the direction of the wind than at right angles to it.

Along coasts and in deserts where there are long stretches of loose sand, wind movements may cause the formation of dunes. The vegetation of dunes is characteristic in that it must be adapted to a change in the form of the dune, brought about by the shifting sand. The most successful dune plants are perennials with long, branched rhizomes, and very long roots. These enable the plant to quickly adjust itself to changes in the depth of sand covering them, as a result of dune movement.

AVAILABLE WATER IN THE SOIL

By far the most important of the environmental factors which have to do with the soil (edaphic factors) is the supply in the soil, of water available to the roots of plants. This depends upon a great many other factors: climatic, edaphic, and biotic. In the chapter on the Root, pages 172–177, the absorption of water from the soil was discussed and something was said of the conditions affecting the available water in the soil. Here we shall enumerate the principal factors determining the quantity of available water and mention some of the effects upon the plant of differences in the quantity.

Principal Factors Influencing the Available Water in the Soil.—

1. The amount of annual precipitation.
2. The distribution of precipitation over the year.
3. The humidity of the atmosphere, since it affects the rate of water loss from the soil by evaporation.
4. The distance of the water table (level of standing water in the soil) below the surface of the soil. The fluctuations in this from one season to another depend chiefly upon the precipitation and evaporation.

5. Rate at which water percolates downward into the soil. This is most rapid in sandy soil, and progressively slower in clay and humus.
6. The power of the soil to raise water from lower levels (the water table) by capillarity. Water is raised much higher by capillarity in clay soil than in sandy soil, but it rises at a more rapid rate in sandy soils than in clay soils.
7. Vegetation. Plants growing in soil may greatly decrease the amount of water in the soil. On account of the water absorbed by the roots of plants and lost by transpiration from them, the soil may lose water much more rapidly than if it were bare.

Fig. 228.

Fig. 229.

Fig. 228.—A giant cactus (*Carnegia gigantea*), an extreme xerophyte, growing in the desert region of southwestern United States.

Fig. 229.—Spanish bayonet (*Yucca whipplei*), a xerophytic plant of the chaparral belt in the mountains of southwestern United States. (Photograph by H. P. Chandler.)

Differences in available water in the soil are practically identical, in their effects upon the plant, with corresponding differences in the humidity of the atmosphere. Dry soil, like low atmospheric humidity, tends to cause a water deficit in the plant.

The importance of the available water in the soil is so great in its effect upon plants that botanists are accustomed to classify plants, as regards their relations to environment, on the basis of their water requirements. For example, they recognize:

1. **Xerophytes.**—Plants which are very resistant to drought or live in very dry places; Russian thistle (*Salsola*), millet (*Setaria italica*), sorghum (*Andropogon*), cactus (*Opuntia* and other genera), sagebrush (*Artemisia tridentata*).
2. **Hydrophytes.**—Plants which live in water or in very wet soil: Cat tail (*Typha*), water lilies (*Castalia, Nelumbo*), sedges (*Carex*).
3. **Mesophytes.**—Plants growing best with moderate water supply: The common plants of meadow and forest.
4. **Halophytes.**—Plants able to grow in salt marshes and alkali flats where there may be an abundance of water in the soil, but where, on account of the high concentration of the soil solution, water is absorbed with difficulty: Greasewood (*Sarcobatus*), salt brush (*Atriplex*), sugar beet (*Beta*), glasswort (*Salicornia*).

AIR IN THE SOIL

The quantity of air in the soil is of considerable importance to plants growing in it. The living cells of the root must have oxygen in order to respire. Respiration is particularly active in the cells of the growing points and the actively growing regions near them. Normally the roots secure the necessary oxygen for respiration by its diffusion into the roots through the root hairs and ordinary epidermal cells. This inward diffusion of oxygen from the soil atmosphere ordinarily goes on readily because of the thinness of the walls of these cells and the absence of a cuticle. A moderately dry soil, not excessively fine in texture, contains much air in its pores. A very wet soil contains less air than would the same soil in a drier condition, for part of the space (larger pores) which would be occupied by water in the wet soil is occupied by air in the drier soil. In a water-soaked soil there is practically no air save that which is dissolved in water. As a rule, the larger the soil particles and the looser and more porous the soil the better its aeration. Most plants die if the soil about their roots is continuously water-soaked—has gravitational water in it. Their death is presumably due principally to insufficient oxygen supply. There are some plants which can thrive although the root system is submerged in water or surrounded by a soil which is water-soaked. Almost all such plants contain in the stem and root

large communicating air spaces. Thus, air absorbed into the leaves and stems may reach the living cells of the root in sufficient quantity. Some, like the bald cypress (*Taxodium distichum*) and various species in tropical mangrove swamps, produce special root branches which grow upward until their ends are above the water level. These special root branches have a central core of loose parenchymatous tissue through which air is said to pass downward to the submerged parts.

The composition of the soil air differs somewhat from that of the atmosphere. The air of the soil is considerably richer in carbon dioxide than that of the atmosphere, this being particularly true of soil occupied by the roots of plants, which give off this gas in respiration.

SOIL TEMPERATURE

The temperature of a soil may very greatly affect the plants which grow in it. One of the principal effects of low soil temperature is the reduction of the rate of water absorption by the root. Plants whose roots are in a soil containing abundant water may wilt if the temperature is very low. Evergreen trees, growing, as most of them do, in regions where the winters are cold, are in considerable danger of water shortage during cold weather; although their roots are unable to absorb much water from a cold soil, their foliage, which is retained throughout the winter, may, on sunny days, transpire considerably. It is probably on this account, and also perhaps because the absence of tracheal tubes from their wood makes it less efficient in water conduction, that these coniferous trees have linear leaves with very thick cuticle and stomata depressed below the leaf surface. These are characteristics of xerophytic plants, and actually, even though they may grow in regions of relatively high humidity and soil moisture, these gymnosperms, such as the pine (*Pinus*), fir (*Abies*), and hemlock (*Tsuga*) are xerophytic plants. In far northern regions and on mountain tops the average soil temperature may be much above the average air temperature. If the soil temperature were as low as the air temperature in such localities, seed-bearing plants would probably not be able to live there at all.

The soil temperature depends upon a great many factors, chiefly (1) the air temperature, (2) the intensity of sunlight, (3) the period during which the sun shines upon the soil, (4) the angle at which the sunlight strikes the soil, (5) the color of the soil, (6) the physical nature of the soil, (7) the amount of water in the soil, and (8) the presence or absence of a soil cover.

QUANTITY AND NATURE OF THE SOIL SOLUTES

Water absorption by the roots can take place only if the concentration of the cell sap of the root hairs is greater than that of the soil water. The adaptations of plants growing naturally in salt marshes or in so-called **alkali** soils resemble those of plants growing in very dry soils or

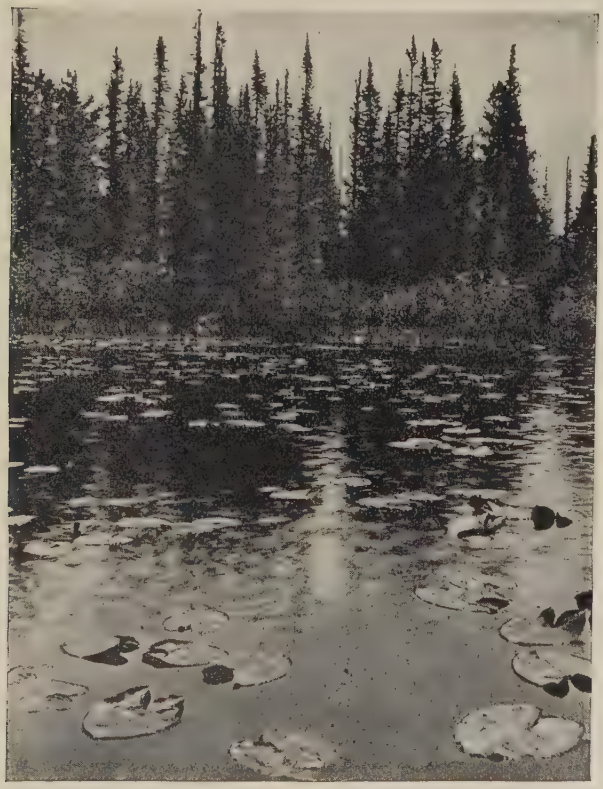


FIG. 230.—A water lily (*Nymphaea*), a typical hydrophytic plant. The rhizome and roots are in the soil beneath the water. The leaves and flowers are brought to the surface of the water by the elongation of their stalks.

in an atmosphere of very low humidity. If the root systems of most plants were exposed to such concentration as exists in salt, swampy, and strongly " alkali " soils, they would not be able to absorb sufficient water to replace that lost by transpiration and would soon die.

The soil water of some soils is deficient in one or more of the essential elements. These elements, it will be recalled, are potassium, calcium,

magnesium, iron, nitrogen, sulphur, and phosphorus. Plants growing in such soils have their growth rate much reduced and remain dwarfed.

Most seed plants thrive best in a slightly acid soil, but there is a wide variation in the tolerance of different plants for acid and slightly alkaline soils. Certain plants, such as sour dock (*Rumex acetosella*) and heather (various *Erica* species), growing normally on quite acid soils, do not thrive in soils which are rich in lime. This is probably due to the fact that such soils are not sufficiently acid.

THE INFLUENCE OF CERTAIN BIOTIC FACTORS UPON PLANTS

Other species of organisms, both plants and animals, are as much a part of the environment of a given plant as are the various climatic and edaphic factors which we have mentioned above. Though in general these biotic factors are second in importance to the factors which have to do directly with soil and atmospheric conditions, they are of great importance, and sometimes (for example, in the case of certain dangerous plant parasites) of greater importance than any other factor in determining whether given individuals or species shall survive in a certain locality.

In nature, plants compete for space, light, water, and inorganic salts. Ordinarily water is lost more rapidly from soil covered with plants than from bare soil. As the result of the competition of plants for the water in a soil, certain species may die off because of excessive drying of the soil by other species which absorb water more rapidly. In a similar manner, there is competition in a forest for light, and the dense shade of the larger plants may prevent the growth of smaller plants which would grow in the locality if it were not for the shading. On the other hand, certain plants which grow well beneath the trees of the forest because the temperature is relatively low there and the humidity high would not be able to grow in that locality if the trees were removed.

Grazing by wild or domestic animals may greatly affect the plants growing in a certain habitat. Most species are unable to survive the constant removal of leaves and parts of the stem by grazing animals. As a result, those plants (principally certain grasses) which are able to withstand cropping and to spread without seed formation tend to take full possession of a closely grazed piece of land.

The soil itself contains many simple organisms, such as algae, bacteria and other fungi, and protozoa. Some of these, particularly certain of the bacteria, raise the fertility of the soil by increasing the amount of nitrogen available for the seed plants growing in it. In the

absence of certain of these organisms, plants belonging to the bean family (*Leguminosae*) remain stunted. Other organisms in the soil may be injurious to seed-bearing plants either because they lessen soil fertility (some of them greatly reduce the available nitrogen) or because they are the cause of root diseases.

Parasitic organisms, bacteria and other fungi, nematode worms, and insects are biotic factors of very great importance. The insect parasite, *Phylloxera*, which at one time destroyed most of the French vineyards, the fungus parasite causing chestnut blight, which has killed many of the chestnut trees of the United States, and the parasitic fungus responsible for the white pine blister rust, which has practically wiped out the white pines of the eastern United States, are particularly striking illustrations of the importance of parasitic plants and animals as living factors in the environment surrounding plants.

This chapter and the preceding one have dealt largely with those features which are common to at least most of the seed-bearing plants. In Part II attention will be directed more particularly to the structural (morphological) and functional (physiological) differences existing between different plants. Instead of limiting ourselves to the Spermatophyta, as in Part I, we shall discuss representatives of each of the four great divisions of the plant kingdom. In addition, an attempt will be made to indicate the general course of evolution by which, from very simple and primitive plants, the complex and highly differentiated Spermatophyta have arisen.

TRANSFORMATION OF MATERIALS AND ENERGY BY THE PLANT

All the features of the universe of which man is aware through his senses may be spoken of in terms of either matter or of energy. Plants are composed of matter, and they absorb, store and transform energy. Their very existence is dependent upon an exchange and transformation of materials and energy. If moving pictures are taken of the plant at work, we see the roots twisting and turning, making their way about, and between the soil particles; we observe the young sprout of the germinating seed lifting the load of soil from its path; we see parts of opening buds moving vigorously; in fact, there is active movement throughout the plant body; and if we examine the interior of the cells; we see the living material, the protoplasm, moving in streams from one part of the cell to another. There are many other activities of plants, besides movement, which involve expenditure of energy. Thus plants, just as truly as animals, actually do work as long as they are alive, and this work requires a supply of energy.

Mention has already been made of the fact that if it were not for green plants none of the animals or chlorophyll-free plants in the world could exist. This is true because the heterophytic plants and the animals are incapable of building up from the simple compounds in the soil and atmosphere the complex compounds of which their bodies are constructed. The formation of these complex compounds, or foods, constitutes the great rôle of green plants in organic nature. The making of foods by plants is of very great significance for two reasons:

1. Because these foods furnish the material out of which the bodies of plants and animals are constructed.

2. Because, in the making of these foods, energy from the sun, which is the world's great source of energy, is stored, and this stored energy can be released within the bodies of the living organisms which make or use the food. The energy thus secured is the only energy which animals or non-food-making plants can use for their life processes. In green plants it is the only energy which can be used for any process except carbohydrate manufacture. Since green plants are responsible for important transformation (1) of materials and (2) of energy, it will be fitting to summarize these changes in material and energy.

The Material which Green Plants Absorb and the Changes which these Materials Undergo.—The principal substances which are taken into the green flowering plant in considerable quantity and which are essential to its proper development are as follows:

From the soil:
- Water
- Salts, containing the following elements:
  - Nitrogen—principally as nitrates but in some cases as compounds of ammonia.
  - Phosphorus—as phosphates
  - Sulphur—as sulphates
  - Potassium, Calcium, Magnesium, Iron } In combination with one of the three preceding elements

From the atmosphere:
- Carbon dioxide
- Oxygen
- Nitrogen (perhaps)

The principal changes which these substances undergo in the plant will be briefly stated.

Water.—In Chapter V, pages 169 to 171, there will be found a statement of the various functions which water plays in the living plant. Most of these functions do not involve, however, a transformation of water

into any other substance, and it is with such changes that we are now concerned. The water used in the process of photosynthesis is so transformed, that is, it ceases to be water and becomes part of the carbohydrate, glucose, which may later be changed into some other sugar or into starch or cellulose or various other substances. The water which passes from the plant during transpiration in the form of water vapor is changed only in its physical form and not (chemically) into another compound. During the process of respiration, sugars are broken down and water is formed again.

Nitrogen, Phosphorus, and Sulphur.—These elements are particularly important as the raw materials, together with soluble carbohydrates, of the proteins and the amino-acids, from which proteins are built up. Proteins contain from 15 to 19 per cent of nitrogen and from $\frac{1}{2}$ to $1\frac{1}{2}$ per cent sulphur. Inorganic nitrogen is elaborated into amino-acids and other nitrogenous organic compounds, chiefly in the leaves. Phosphorus is found in some proteins, particularly the nucleo-proteins of the nucleus, which contain from 0.3 to 3 per cent of that element. Inorganic phosphates are changed to organic phosphorus compounds principally in the leaves. There is no evidence that animals are able to use nitrates, sulphates, and phosphates to build up their own amino-acids or proteins. These latter substances are just as essential to them as to plants, but they are all secured directly or indirectly from plants. The nitrogen, sulphur, and phosphorus which are absorbed by the plant (and the same is true of potassium, calcium, magnesium and iron) never leave the plant except when parts of the plant (leaves, fruits, flowers or broken branches) are separated from it. If proteins containing these elements are broken down in the plant, the simple compounds resulting are not excreted as is nitrogen in the form of urea by the higher animals. Instead, they are again used for the building up of proteins and amino-acids.

Potassium, Calcium, Magnesium and Iron.—Though all of the higher plants must be supplied with these substances, we have little knowledge of the changes which the simple inorganic compounds of these elements undergo within the plant. Part at least of the magnesium is used in the making of chlorophyll *a* and chlorophyll *b*. Iron is also essential to chlorophyll formation, although the chlorophyll molecule contains no iron. Iron is also considered as the catalyst concerned in oxidation processes in the plant. It may be that potassium, calcium, and iron perform their essential function without change from the simple inorganic form in which they exist in the soil solution.

Carbon Dioxide.—Carbon makes up from 40 to 50 per cent of the dry weight of all plants, and the gas carbon dioxide, is the source of all

this carbon. The carbohydrates are utilized in the making of proteins and fats. When sugars and fats, which are the principal respirable materials in the plant, are respired, carbon dioxide is again formed and liberated into the atmosphere. When plant parts die, the sugars, starch, cellulose, fats, and all other organic compounds are broken down by bacteria and other fungi and the carbon is finally set free from these compounds in the form of carbon dioxide. Thus there exists in nature a carbon cycle in which the carbon of carbon dioxide is continuously being built up into complex foods, which are again broken down with the formation of carbon dioxide. Green plants, animals, and bacteria and other fungi may all play a part in this carbon cycle. In Chapter XII will be found a brief account of this cycle and a diagram illustrating the part played by different organisms.

Oxygen.—Carbohydrates, protein—in fact all essential substances in the plant—contain oxygen in combination with other elements. This oxygen is derived for the most part from water or from carbon dioxide used in photosynthesis. But the plant also absorbs the free oxygen of the atmosphere. This is utilized solely for the oxidation of sugars and fats in respiration and becomes part of the products of respiration.

Nitrogen.—Some simple green plants, such as some algae and certain bacteria, are able to use as nitrogen for protein manufacture the free nitrogen gas of the atmosphere. There is some evidence to indicate that this same power may be possessed in slight degree by some of the seed-bearing plants. However, there can be no doubt that under natural conditions most of the nitrogen used in the formation of nitrogenous foods in the seed-bearing plants is secured from the soil in the form of compounds of nitrogen with other elements.

RÔLE OF THE ELEMENTS WHICH COME TO THE PLANT FROM THE SOIL

Element.	Chief Rôles.
Nitrogen	(*a*) Constituent of all proteins, which are essential components of protoplasm. (*b*) Lack of nitrogen results in a stunted plant. (*c*) Abundance of nitrogen tends to produce rank vegetative growth, and to retard date of maturing of plant.
Phosphorus	(*a*) Constituent of proteins, particularly those of the nucleus. (*b*) Transformation of insoluble carbohydrates to soluble carbohydrates does not take place in absence of phosphorus. (*c*) Abundance of phosphorus tends to hasten the maturing of the plant and stimulates production of seed.
Potassium	(*a*) Photosynthesis and translocation of carbohydrates dependent upon presence of potassium. (*b*) A deficiency of potassium is associated with a lack of carbohydrate reserve.

Element.	Chief Rôles.
Calcium	(*a*) Apparently stiumulates root development.
	(*b*) A deficiency of calcium retards transportation of carbohydrates, and their utilization.
Magnesium	(*a*) A component of the chlorophyll molecule; a deficiency of magnesium is attended by **chlorosis.**
	(*b*) Essential to formation of fats.
	(*c*) Aids in the transport of phosphorus from older to younger parts of the plant.
	(*d*) A deficiency of magnesium is attended by a reduction in fruit formation.
Iron	(*a*) Essential to chlorophyll formation (not a part of chlorophyll molecule, however). A deficiency results in **chlorosis.**
Sulphur	(*a*) Essential to the formation of proteins.
	(*b*) A deficiency of sulphur results in retarded cell division and suppression of fruit development.

In addition to the ten elements--carbon, hydrogen, oxygen, nitrogen, sulphur, phosphorus, potassium, magnesium, calcium and iron—long recognized as essential to the continued growth and development of green plants, there are certain other elements, which are known to be beneficial or indispensable. For example, it has been found that **manganese, boron,** and **zinc** are essential to the growth of a number of different kinds of green plants, but that very small amounts suffice. Our failure to recognize earlier that certain of these elements are essential is due to two facts. First, that they are needed only in very small quantities and second, that the " chemically pure " compounds used in preparing culture solutions in the past have generally, or at least frequently, contained unsuspected traces of these elements quite sufficient in quantity to supply the needs of the plant's growth in culture.

Other elements concerning which there is some evidence indicating their importance to particular plants are: **silicon, sodium, chlorine, aluminum, bromine** and **iodine.**

Energy Changes Brought about by the Plant.—We have already learned that certain chemical changes, for example, burning and respiration, are attended by liberation of energy.

It is one of the principal rôles of green plants to take certain of the simple compounds (carbon dioxide and water) in which no available energy is stored and build them up into substances in which there is stored or potential energy. It is the energy of sunlight which is thus stored by green plants. These substances produced by plants are the source of all energy which is used by animals within their bodies, and by heterophytic plants. Moreover, if we except the energy of falling water and wind, and that of the tides and waves which we may sometime be able to utilize, **all the energy which is used by man for any pur-**

pose is secured from the energy stored in the substances made by plants. Our principal fuels, wood and coal, are unmistakably plant products. All the explanations of the origin of petroleum agree that directly or indirectly it also has been produced by green plants. The energy set free in the form of heat when these fuels are burned can be changed into mechanical energy by the steam engine or gasoline motor. This in turn may be transformed into electrical energy by the dynamo, and this again into light energy by the electric lamp or into heat again by the electric stove. But whatever form it may take, the energy secured by the combustion of coal, wood, or petroleum is but the energy of sunlight which perhaps hundreds of centuries ago was absorbed by green leaves when carbon dioxide gas and water were being united to produce the energy-storing substances from which these fuels were formed. Green plants are then preëminent not only as makers of substances essential for the building and repair of the bodies of all organisms but also as the storers of the sun's energy for use within the bodies of organisms, and for use in the industries. The amount of energy which can be secured from other sources than the combustion of the products of photosynthesis is only a small fraction of that used in industry. Man is accordingly, and may always be, dependent upon green plants for much of the energy used in the industries, as he is also for all the energy used within his own body. The following is a brief statement of the energy changes involved in the life of a green plant in the utilization of their products.

I. Radiant energy of sunlight falls upon green leaves.

II. A large part of this is absorbed by the leaves (in some cases at least as much as 80 per cent).

1. Part of this is changed to heat, raises the temperature of the leaf, and is lost to the air if the air is cooler than the leaf.
2. Part of it, after change into heat energy, is used changing water into water vapor during transpiration.
3. Part of it (probably never more than 7 or 8 per cent of the total energy falling upon the leaf) is used in photosynthesis and stored in the carbohydrate molecules.

III. The energy stored in that part of the carbohydrate which is transformed into cellulose is not liberated until the cellulose is burned or decays.

IV. The sugars in the plant are in part respired and their stored or potential energy is freed.

1. Of this freed energy a relatively small part is in the form of heat and is lost.
2. The remainder of the energy freed by the respiration of sugar

is used for various processes taking place within the plant—for instance, in the building up of proteins from carbohydrates.

V. Sugars, or compounds formed from sugars, are used as food by animals or plants which can not make food. These are in part respired by these organisms and furnish heat and other forms of energy necessary for the life processes. In the case of the higher animals, the heat produced is not all wasted but maintains the temperature essential to the health of the animal.

VI. Dead plant tissue or plant products may decay. In that case carbohydrates or other energy-storing substances are broken down by the bacteria and other fungi (non-food storing plants) which cause decay, that is to say, these substances are respired by the organisms of decay and liberate energy, partly as heat and partly in other forms used by the bacteria and other fungi.

VII. Dead plant tissue or plant products, when burned as fuel, free energy as they are broken down into carbon dioxide, water, and other simple compounds.

PLANT ASSOCIATION

Rarely in nature do individual plants grow isolated from other individuals of the same species. On the contrary, plants, like human beings and other animals, generally live in associations, groups or communities, such as forest and meadow. This community life among plants, as among animals, is largely a response of individual plants to a given set of environmental conditions. We may speak of a black spruce community, a maple-birch community, a water-lily community, and so on. Those communities are very seldom made of individuals of a single species only. Even though the community is designated by the name or names of one or a few of the most prominent (dominant) species, a considerable number of species is almost always present. Plant communities or associations such as a yellow pine forest or a sphagnum swamp generally owe their origin largely to the existence in a given location of environmental conditions particularly favorable to the species which they include or at least unfavorable to species with which they would be forced to compete in other locations. At the same time a plant association once established may have a marked influence upon its surroundings. It may modify the texture and water content of the soils and the amount of soil salts; and to a certain degree it may alter light, humidity, temperature, and air movement in the vicinity. This is true not only of natural plant associations but also of those artificial plant associations established and maintained by man. Thus windbreaks may greatly reduce water loss from the soil on their leeward side, and a

heavy crop of corn will change considerably the quantities of various mineral salts in the soil. So it is that just as the environment affects the character of vegetation, the vegetation may to some extent react upon the environment. While it is important to know what influence certain soil conditions have upon the growth of our crop plants, it is often as important to understand what effect a given crop is going to have upon the soil and this upon crops which follow it. Our orchards, fields, and gardens are cultivated communities of plants. Many problems arise as to the best methods of handling these communities, and these problems may be quite different from those which arise in connection with the individual plant.

Plant Invasion.—There is a tendency for plant individuals and plant communities or associations to extend their areas of distribution; this implies the invasion of new territory. For example, the seeds from an individual plant may be carried by various agencies such as wind, or birds, to places more or less remote from the parent. If the seeds find in these new areas conditions suitable for their germination, and if the plants can adjust themselves to the habitat, grow to maturity, reproduce and finally become established there, then invasion is complete. Striking examples of the invasion of a species are furnished by certain weeds. Seeds of the Russian thistle found their way into the United States in 1873 in flaxseed brought from Russia and sown near Scotland, South Dakota. As a result of its excellent means of seed dispersal and its ability to become established in a variety of soil and climatic conditions, as well as to the absence in its new homes of its natural competitors which were not imported with it, the Russian thistle has invaded a large part of western United States.

A plant association such as a forest may also invade territory and displace another association. For example, a burnt-over mountain slope, temporarily occupied by an herbaceous growth, may be invaded by the dominant tree species of the region, together with their plant associations, and a characteristic forest growth come to occupy the area.

There are in nature various barriers, which prevent species or plant communities from extending their geographical range. These may be either physical or biological. Deserts, mountain ranges, and large bodies of water are physical barriers. For example, hydrophytic and mesophytic species cannot successfully invade a desert and spread to suitable habitats beyond. Vegetation is a biological barrier. A dense forest, for example, is a barrier to the invasion of light-demanding species, which are prevented by the forest from extending their distribution in that direction.

Certain species of plants are said to be **endemic,** that is, are confined to restricted areas. For example, the redwood (*Sequoia sempervirens*) is now restricted to a narrow strip, the "fog belt" along the western coast of the United States.

Plant Succession.—A plant association existing in a given location does not necessarily remain permanently in possession of the area in question. Thus if we observe over a period of years the vegetation of an area, small or large, we may note that its character changes; that there may be a succession of plant communities, one replacing the other, and successively occupying the same area. In some cases such succession goes on at too slow a rate to be observed within a single lifetime. The following three types of succession of associations have been recognized:

1. *Regional successions,* due to widespread climatic changes.
2. *Topographic successions,* due to changes in topography resulting from erosion or deposition of material, as at the base of cliffs or at the mouths of streams.
3. *Biotic successions,* due to plant and animal factors, such as the accumulation of humus.

An example of an extensive regional succession is the invasion, following the glacial period, of southern species into those regions which experienced marked climatic changes due to the recession of the continental ice sheet

Topographic successions are more rapid than regional successions. They are well illustrated in the development of flood plains along rivers, where erosion and deposition of sediment bring about progressive changes in the habitat which result in corresponding progressive changes in the vegetation.

Biotic successions are seen to advantage in the filling of ponds and lakes, where there is an accumulation of humus, resulting from the death of the plants. The original aquatic vegetation is displaced by swamp vegetation, and this in turn by a mesophytic type.

After a period of years, during which there has been a succession of plant communities, a type of community finally occupies the area which remains unchanged in its principal features. We speak of this as the climax vegetation of the region, and it is determined chiefly by the climate. For example, in the eastern United States, the gradual leveling of xerophytic ridges and the filling of lowlands and valleys culminates in a mesophytic deciduous forest. In southwestern United States, on the other hand, the climax vegetation is that of a desert.

PART II

CHAPTER X

INTRODUCTION

Point of View.—In the first part of this volume we have discussed the form and anatomy of the various organs of the plants belonging to the Spermatophyta, the highest of the four divisions (see page 13) into which the plant kingdom is usually divided, and have given an account of the physiological processes going on in these plants.

In the second part we shall be concerned, for the most part, with the other three divisions of the plant kingdom, the Thallophyta, the Bryophyta, and the Pteridophyta. In our study of these plants and of a few representatives of the Spermatophyta, we shall attempt to emphasize the following considerations:

1. The probable course of evolution from the simplest plants through forms of increasing complexity to the seed plants, which are the most highly organized of living plants.

2. The great variety in form and structure of the organisms making up the plant kingdom.

3. The peculiarities in structure, and particularly in function, by which many of the simpler plants manage to live successfully under conditions very different from those surrounding typical seed plants.

4. The importance of certain simpler plants, particularly the bacteria and other fungi, in relation to health and to agriculture and other industries.

5. The function of reproduction in plants and particularly the mechanism of inheritance, i.e., the processes which determine what part of the chromatin in the nuclei of the new plant shall be furnished by each of the parent plants. (This is the basis of our knowledge of genetics and of the practice of plant breeding.)

6. The principal laws of heredity and of evolution as illustrated by plants.

THE MEANING OF PLANT RELATIONSHIPS

There exist in the world to-day about a quarter of a million different kinds of plants which have been described and named, and the number

of named species of animals is much greater, nearly a million. New species are constantly being discovered by the systematic botanist and zoologist.

Among this great variety of different kinds of organisms there are many groups of species which obviously resemble each other more than they do any other kinds of organisms. Familiar examples of groups of similar species which are recognized even by those who are not given to accurate observations of plants are the oaks, all of which bear acorns and most of which have pinnately lobed leaves; the mints, which generally have square stems and whose foliage often has an aromatic odor; the beans, peas, and similar plants, whose fruits are pods or legumes and whose flowers are of a form which suggests a butterfly; and the toadstools and mushrooms with their stalked, umbrella-shaped caps. A careful comparison of the organisms about us would reveal, even to one without special knowledge, many more such groups of strikingly similar plants.

Both the existence of so many different kinds of organisms and the striking similarity between the members of such groups as have just been mentioned demand an explanation.

We have already referred to the two explanations which have been offered in the Introductory Chapter at the beginning of this volume. The first is the Theory of Special Creation, which assumes that each species that exists or ever existed was separately created, and that each of the specially created individuals of a species was endowed with the power of producing other individuals like itself, but was without ability to give rise to individuals differing from it. This theory does not furnish any explanation of the close resemblances which exist between certain kinds of organisms.

The second explanation is the Theory of Organic Evolution. So closely is the name of Charles Darwin associated with this theory that many persons without biological training believe that the theory originated with him. Actually it had its beginning as early as the time of the Greek philosophers, long before the beginning of the Christian era, and it was clearly and comprehensively stated by Lamarck, who was born more than sixty years before Darwin. Darwin was one among many scientists of his time who accepted the theory of organic evolution. His special service lay in his attempt to work out the factors in nature by which organic evolution has been brought about. In a subsequent chapter we shall give an account of his work and of later attempts to discover how the evolution of plants and animals goes on.

Evolution is a process in which great differences arise through a succession of slight changes. It is clear that such a process is constantly

going on among other things besides plants and animals. History teaches us that present-day governments, methods of education, agriculture, medicine, manufacturing processes, dress, machinery, weapons, methods of warfare, means of communication, and everything else in our modern civilization have come about through evolution. History is indeed merely an account of the evolution of human institutions, arts, and practices. Inorganic evolution (the evolution of other things than organisms) is illustrated by the collections, which may be found in many great museums, showing the history of development in human apparel, implements of various sorts, optical instruments, etc. Within our own life many of us have witnessed practically the whole course of the evolution of the flying machine and methods of wireless communication. The geologist can inform us very fully in regard to the evolution of the hills, valleys, streams, and other features of the regions in which we live, and the astronomer knows much of the evolution of our earth and other planets and of the sun and stars.

It is, however, with the evolution of organisms (organic evolution) that we are here concerned. The now generally accepted explanation of the great number of plants and animal species, and of the close similarity existing between some of these, is called the Theory of Organic Evolution.

The principal features of this theory are briefly these:

1. The existing kinds of plants and animals and all the kinds that are now extinct, with the exception of one or a few original and very simple forms, have arisen from preëxisting kinds by relatively slow changes.

2. If the preceding proposition is true, it follows that all the different kinds of plants and animals are related.

3. Those species which are similar in many particulars are closely related, that is, they are not separated by many forms from a common ancestor (species) from which they have all descended.

4. Although it is natural to look upon evolution as **progressive,** that is, as such that it results in an increase in complexity and differentiation, it may often be retrogressive and result in a development of forms having less complexity and differentiation than their ancestors.

If we could secure specimens of all the kinds of plants and animals which now exist or which ever have existed, it should be possible by comparison of their structure to work out the whole course of evolution. Many species of plants and animals have become extinct. This extinction has in the case of a few species actually taken place since man has been studying plants and animals, and thousands of kinds of organisms died out before the animal species we call man was himself evolved. In

the rocks we find the remains of some of these extinct plants and animals as fossils. These remains are in many cases mere fragments of the bodies of these organisms, and it is probable that fossil remains of many of these extinct plants and animals, particularly of the simpler and more primitive forms, will never be found.

CLASSIFICATION OF PLANTS

In spite of the fact that our knowledge of the extinct species, and of living species too, is very incomplete, it is possible for us to trace with considerable certainty the course of evolution within certain groups of related plants. Thus we arrive at a natural classification of such groups. Our conclusions in such cases are largely based upon a comparison of the structure and development of the plants or animals in question. Experience teaches us, however, that certain resemblances between different species are not to be considered as evidence of their close relationship. Thus the fact that a fly and a sparrow both have wings is no basis for the conclusion that these two winged animals are more closely related to each other than they are to any wingless animals. Though the wings of these two kinds of animals are superficially alike, since they are organs adapted to the same function, a study of their structure and development shows that in most respects they are dissimilar organs. The wing of the fly is in a reality a flap of skin, while the wing of a bird corresponds to the fore limbs of the quadrupeds. Organs which are superficially similar merely because adapted to the same function, but which have not been evolved from one structure possessed by some common ancestor are said to be **analogous.** Organs such as the wing of a bird and the fore limb of one of the higher animals, which, though perhaps differing in function, have had a common origin in evolution are spoken of as **homologous.** Thus, as we shall later show, the leaves of a moss plant and of a tree are analogous but not homologous, whereas the scales of a pine cone and the leaves of a maple are presumably homologous.

Characteristics Used as Bases for Plant Classification.—Since we shall be concerned to some extent, in the following chapters, with the relationship of the various plants discussed, we may well mention a few of the characteristics of plants which are used to determine relationship and therefore as a basis for classification. These vary in their value in different groups of plants.

1. *Cell Structure.*

One of the simplest groups of plants (the blue-green algae or *Cyanophyceae*) is made up of cells which, with few exceptions,

have no nuclei. There is considerable reason to believe that they are rather closely related to the Bacteria, which are also without definite nuclei. Other examples might be cited in which similarities of cell structure seem to indicate relationship.

2. *Arrangement of Cells.*

In some of the very simple plants, each cell division is followed by a separation of the daughter cells, so that an individual plant consists of a single cell; in others the cells remain together in pairs; in others they form filaments, sheets of cells, or cell groups of various shapes. Although all these different types of cell arrangement may occur in different groups of plants, they often do indicate the relationship of species within one of these groups.

3. *Presence or Absence of Certain Vegetative Organs and Tissues.*

The possession of roots by all the Pteridophyta is probably an indication that these plants are more closely related among themselves than are any of them to the mosses or other rootless plants. The absence of tracheal tubes from the wood of most Gymnosperms indicates that these plants are more closely related among themselves than they are to the Angiosperms, in most of which tracheal tubes occur.

4. *Similarity of Reproductive Structures.*

Comparison of the flower parts or of other structures connected with sexual reproduction is one of the most used and most dependable bases for judgment as to the relationship of plants. The vegetative structures of closely related plants may be adapted to very different environmental conditions and so may be dissimilar. Their reproductive structures, on the other hand, being shorter-lived, are subjected for shorter periods to enrivonmental factors. In general, their relation to the environment is not so close and they are therefore less likely to change in response to differences in the environment. Reproductive structures are more conservative than vegetative organs and are therefore more dependable as indicators of relationship.

A decision as to the relationship of two species or plant groups is generally based upon several similar characteristics. A single characteristic, especially if it relate to vegetative structure, is in many cases not considered a safe bases for judging relationship, for similarity or

difference in respect to this characteristic may be due to the influence of environment.

Our knowledge of plants is too incomplete for us to work out a natural classification which will show the real relationships of all plants. Accordingly, the classifications of plants which we use are in part natural and in part artificial. Systematic botanists are constantly endeavoring to increase our knowledge of the evolution of the plants with which we are acquainted and thus to approach more nearly to the ideal of a complete natural classification. One of the most widely used classifications is in part as follows:

A Classification of the Plant Kingdom

Rank.	Scientific Names of the Groups.	Common Names.
Division I.	*Thallophyta*	*Thallus plants*
Subdivision 1.	Algae—	
Class 1	Cyanophyceae	Blue green Algae
Class 2	Chlorophyceae	Green Algae
Class 3	Phaeophyceae	Brown Algae
Class 4	Rhodophyceae	Red Algae
Subdivision 2.	Fungi—	
Class 1	Bacteria	Bacteria
Class 2	Myxomycetes	Slime Fungi
Class 3	Phycomycetes	Algal Fungi
Class 4	Ascomycetes	Sac Fungi
Class 5	Basidiomycetes	Club Fungi
Division II.	*Bryophyta*	*Moss Plants*
Class 1	Hepaticae	Liverworts
Class 2	Musci	Mosses
Division III.	*Pteridophyta*	*Fern Plants*
Class 1	Filicineae	Ferns
Class 2	Equisetineae	Horse-tails
Class 3	Lycopodineae	Club mosses and related plants
Division IV.	*Spermatophyta*	*Seed Plants*
Class 1	Gymnospermae	Conifers and related plants
Class 2	Angiospermae	Higher flowering plants
Subclass 1.	Dicotyledones	Dicotyledons
Subclass 2.	Monocotyledones	Monocotyledons

The two groups (Algae and Fungi) into which the first division of the plant kingdom is subdivided are artificial groups based upon the manner in which these plants secure their food. The algae with few exceptions are able to carry on photosynthesis and are therefo e inde-

pendent of any other organisms. The fungi, on the other hand, must, like animals, secure their food ready made. That is, the algae are **autophytic** and the fungi **heterophytic.** Actually, however, some of the fungi are no doubt more closely related to some of the algae than they are to certain other species of the fungi, and certain algae are more closely related to certain fungi than they are to certain other algae.

The following recently proposed classification is in many respects preferable to the classification given above. In cases where the group names differ from those used in the first classification the equivalents are given in parentheses.

Rank	
Kingdom	Phyta (The Plant Kingdom)
Subkingdom 1	Sporophyta (Thallophyta)
Class 1	Phycophyta (Algae)
Subclass 1	Myxophyceae (Cyanophyceae)
Subclass 2	Chlorophyceae
Subclass 3	Melanophyceae (Phaeophyceae)
Subclass 4	Rhodophyceae
Class 2	Mycophyta
Subclass 1	Myxomycetes
Subclass 2	Schizomycetes (Bacteria)
Subclass 3	Eumycetes
Division 1	Phycomycetes
Division 2	Mycomycetes
Subdivision 1	Ascomycetes
Subdivision 2	Basidiomycetes
Subkingdom 2	Embryophyta
Class 1	Bryophyta
Subclass 1	Hepaticae
Subclass 2	Musci
Class 2	Pteridophyta
Subclass 1	Filicineae
Subclass 2	Equisetineae
Subclass 3	Lycopodineae
Class 3	Spermatophyta
Subclass 1	Gymnospermae
Subclass 2	Angiospermae
Division 1	Dicotyledones
Division 2	Monocotyledones

In the widely used classification of Engler and Prantl the Plant Kingdom is divided into thirteen divisions of which the first eleven include the plants commonly included in the Thallophyta. The twelfth

includes all the plants generally included in the Bryophyta and Pteridophyta and the thirteenth corresponds to the Spermatophyta.

Frequently the Thallophyta, Bryophyta and Pteridophyta are spoken of collectively as the *Cryptogams*, the term *Phanerogams* being applied to the Gymnospermae and Angiospermae. Many botanists use the term Archegoniatae for the Bryophyta and Pteridophyta.

CHAPTER XI

THALLOPHYTES—ALGAE

CHARACTERISTICS OF THE THALLOPHYTES

The name Thallophyta means thallus plants, a thallus being a plant body without true roots, stems, or leaves. There are, however, thallus plants in other divisions besides the Thallophyta, and in some plants belonging to the Thallophyta there are structures which resemble superficially the roots, stems, and leaves of the flowering plants and which perform the same functions, at least in part.

Whereas the Bryophyta, Pteridophyta and Spermatophyta are clearly marked groups within each of which there is a marked uniformity in many characteristics, so great is the variety of plants included in the Thallophyta that it is very questionable whether they should be included in a single group coordinate with the Bryophyta, Pteridophyta and Spermatophyta. Actually they have little in common save the small size and simplicity of most of them.

The Thallophyta include the simplest of plants. In size they vary from bacteria, many of which have a diameter of less than $\frac{1}{2000}$ millimeter, to the giant brown seaweeds of our California Coast, which may be several hundred feet long. Typically, the Thallophyta are aquatic plants, but most of the fungi, though preferring moist locations, do not thrive if submerged in water.

The multiplication and distribution of thallophytes is generally accomplished by means of asexual spores. These are single protoplasts, naked or surrounded with a cell wall, which, after becoming separated from the plants producing them, can develop into new individuals.

Methods of Reproduction.—As already stated, the reproductive structures and processes of plants are of very great importance in determining their relationships. Within each of the three higher divisions of the plant kingdom there is a general similarity in methods of reproduction, but among the motley assemblage making up the Thallophyta there is great variety in this respect. Reproduction in these (as in the other subdivisions) may be either by the asexual or the sexual method. In the former method each new individual is the product of a

single parent plant, while in the sexual method each new individual develops from a cell (the **zygote**) which is the product of the fusion of two protoplasts generally originating in different parent individuals.

Asexual Reproduction.—Fission.—The simplest form of asexual reproduction is called **fission.** It is restricted to unicellular organisms and is the sole method of reproduction employed by the most primitive plants. It consists merely in the division of a single-celled individual into two new single-celled individuals of equal size. These two new individuals, produced by fission, together contain all the materials of the single parent cell. Organisms which reproduce solely by this method, therefore, never die except as the result of shortage of food or water or other unfavorable external conditions. Natural death (death from old age), such as most plants and animals experience, does not take place among these forms. This is the method by which bacteria reproduce. Under favorable conditions some species of bacteria may undergo fission as often as every twenty minutes.

Asexual Reproduction by Spores.—Asexual spores may be non-motile or capable of active locomotion by means of whip-like filaments of protoplasm called **cilia.**

(*A*) The motile asexual spores are called **zoospores.** There are other motile cells produced by plants, but zoospores are the **only motile protoplasts that are able to develop directly into new individuals.** Zoospores do not have any cell walls but simply consist of a naked mass of protoplasm. In some cases the entire protoplast of a vegetative cell escapes as a single zoospore; in other cases the protoplast of a vegetative cell divides into two or more protoplasts, each of which develops one or more cilia and becomes a zoospore.

(*B*) Non-motile asexual spores often consist of a vegetative cell which has grown in size and thickened its wall. Such spores are produced by *Nostoc* and *Cylindrospermum* (Fig. 234) and other algae. In other cases, especially among the fungi, the non-motile asexual spores are special cells and are produced within an organ called a **sporangium.**

Sexual Reproduction.—The protoplasts which fuse to form the zygote in the process of sexual reproduction are called **gametes** (Fig. 238, E). They are almost always naked protoplasts, having no cell wall. In the blue-green algae, in many other simple algae, and in the bacteria there is no sexual reproduction. In the most primitive cases of sexual reproduction in plants, the gametes are all alike in size and structure. Such gametes are called **isogametes.** They are generally motile, having cilia, like zoospores. The gametes are, however, usually unable to produce new individuals until they have fused in pairs. It is customary to speak of the fusion of isogametes as **conjugation,** and of the resulting

zygote as a **zygospore.** The protoplast of the zygospore forms around itself a cell wall which soon becomes much thickened and protects the protoplast within. The zygospore generally remains in a resting condition for some time before it **germinates.**

Most Thallophyta and other plants having sexual reproduction do not have isogametes but produce two kinds of gametes (**heterogametes**). These heterogametes may differ merely in size, the smaller ordinarily being more active than the larger. Generally, however, the larger gametes are without cilia and therefore incapable of locomotion. The smaller, active gametes, which are called **male gametes,** are produced in much greater numbers than the larger **female gametes,** which are known as **egg cells** or **oospheres** (Figs. 247 and 251). In plants which produce heterogametes the zygote is formed by the fusion of a male gamete, or **sperm,** with a female gamete, or egg cell, and never by fusion of two gametes of the same sort. The zygote resulting from the fusion of heterogametes is called an **oospore.** The actual fusion is called **fertilization.**

Oospores generally become surrounded by a thick wall, as do zygospores, and in most cases do not germinate and develop into new plants until after a period of dormancy. Zygospores, oospores, and asexual spores generally germinate in much the same manner. If they are resting spores, capable of remaining dormant for some time, their protoplasm generally contains much less water than does active protoplasm. When the conditions for germination are favorable, water is absorbed through the spore wall by the enclosed protoplast. The resulting swelling of the protoplast ruptures the spore walls, and a part of the protoplasm extrudes through the opening. The protoplasmic projection soon forms an enclosing cell wall which, with the contained protoplasm, is called the **germ tube.** This tube continues to grow, and in most cases its contents divide to form a number of cells from which the new plant develops.

The following is a summary of methods of reproduction in Thallophyta, and indicates the spore types involved.

Asexual Reproduction—(without union of protoplasts).

(*a*) Fission—division of a single-celled individual into two new individuals of equal size (Fig. 231).

(*b*) Asexual spore formation—motile asexual spores or zoospores (Figs. 245, and 250) and non-motile asexual spores (Figs. 234 and 280).

Sexual Reproduction—(with union of protoplasts).

(*a*) Conjugation—the fusion of similar gametes (isogametes) to form a zygospore.

(*b*) Fertilization—the fusion of dissimilar gametes (heterogametes) to form an **oospore.**

The Thallophyta consist of two subdivisions, the **algae** and the **fungi.** The algae are the **autophytic** thallophytes, that is, they are able to build up their own foods out of inorganic materials, such as carbon dioxide, water, and simple mineral substances. The fungi are **heterophytic** thallophytes, that is, they must secure food directly or indirectly from other organisms. Among the algae there are a few species which have lost the ability to make their own food but which show in their structure such unmistakable evidence of close relationship to typical algae that we include them among the algae in spite of their heterophytic habit.

ALGAE (AUTOPHYTIC THALLOPHYTA)

Characteristics of the Algae.—With very few exceptions, the algae possess chlorophyll, although many of them, particularly the red algae and the brown algae, are not green in color because of other pigments which are associated with the chlorophyll and mask its green color.

The great majority of algae are aquatic, though some grow on soil and a few others on the stems of trees or upon other objects exposed to the air. Algae make up the greater part of the vegetation of the ocean. The free-floating marine plants are generally unicellular forms and are spoken of collectively as the **phytoplankton** of the sea, plankton being a collective name for free-floating aquatic animals and plants. Those growing near the shore line or in shallow parts of the sea constitute the **phytobenthon** of the sea. (**Benthon** is a collective term for attached aquatic plants and animals.) These plants are mostly algae (" kelps " and other " seaweeds "). Algae are also common in bodies of fresh water, both as plankton and benthon plants. There is a great range of size and complexity among the algae. The smallest are microscopic, unicellular plants and the largest are made up of millions of cells and may be several hundred feet in length. The plant body of these large forms is made up of various organs within which there is considerable differentiation of tissues.

The Four Classes of the Algae.

Blue-green algae	(Cyanophyceae)
Green algae	(Chlorophyceae)
Brown algae	(Phaeophyceae)
Red algae	(Rhodophyceae)

The names of the four classes of the Algae are based upon the characteristic differences in color. However, the color differences are not the sole nor the most important ones. The members of each class have certain characteristics in common, such as cell structure, reproductive processes, etc., which in general are more dependable as indicators of relationship than is color. There are in fact some Cyanophyceae which are brown, some Chlorophyceae which are red, and some Phaeophyceae and Rhodophyceae which are green.

THE CYANOPHYCEAE

Characteristics of the Cyanophyceae.—The plants of this class are made up of cells which are without definite nuclei and, with the possible exception of three or four genera, without any distinct chloroplasts. The pigments of the cells are generally restricted to the outer region of the protoplast, but this colored part is not sharply marked off from the colorless protoplasm within, which is called the **central body.** The central body has been called an " incipient nucleus," and may represent a stage in the evolution of a true nucleus. It contains in all cases granules of chromatin or a similar material which probably plays the same rôle as the chromatin of the nuclei of most plants. The cell walls of the Cyanophyceae consist, as a rule, not of the carbohydrate, cellulose, but of **chitin,** a nitrogen-containing substance which is found in the cell walls of bacteria and in many animals, particularly insects. In addition to chlorophyll the plants of this group generally contain one or more **accessory pigments,** the commonest of which is a blue pigment called **phycocyanin.** It is soluble in water and can easily be separated from the green pigment, which is not water-soluble but can readily be extracted with alcohol. A red accessory pigment is present in some forms, so that there are " blue-green " algae which are red. One such form, *Trichodesmium erythraeum,* is a floating marine plant which gives a bright red color to the water when present in large quantities. The Red Sea owes its name to the occasional coloring of its waters by this organism. Almost all Cyanophyceae secrete considerable quantities of a gelatinous substance which forms a sheath or matrix around the cells or cell groups.

The product of photosynthesis in the Cyanophyceae is not starch or glucose but another carbohydrate, glycogen, which is also found in many fungi and frequently in animals.

There is no sexual reproduction in the Cyanophyceae.

Distribution of the Cyanophyceae.—These plants are abundant in fresh and in brackish water and many forms are found in the sea.

They are important elements in the plankton and benthon. A number of forms are abundant in moist soil, especially when it is rich in organic matter. They form the principal vegetation of hot springs, where they have been found living in water as hot as 87° C. A few plankton forms are exceedingly troublesome in reservoirs, giving a disagreeable flavor to the water.

Certain of the Cyanophyceae are associated with fungi in the formation of lichens, although most lichens are associations of green algae (Chlorophyceae) and fungi. This association of autophytic and heterophytic organisms in the lichens is believed to be of mutual benefit to both. Such a relation between two organisms is called **symbiosis.** The food of lichens must clearly be supplied by the algal component, but the fungus is believed to assist the alga by reason of its ability to absorb moisture from the air and retain it tenaciously. Colonies of certain blue-green algae grow within the thallus of *Anthoceros*, one of the Bryophyta, and in the roots of a Spermatophyta, *Cycas*. It is doubtful whether the relation in these two cases is one of mutual benefit.

In moist regions Cyanophyceae are abundant on the trunks and branches of trees and on rocks, and their presence is an important factor in the coloration of the landscape. In waters which are contaminated by sewage or which contain large quantities of organic matter from other sources, the blue-green algae are often abundant. There is still some doubt as to whether this is due to the ability of these plants to use organic matter from the surrounding medium as food, or to the fact that other algae with which they must ordinarily compete can not grow in such polluted waters.

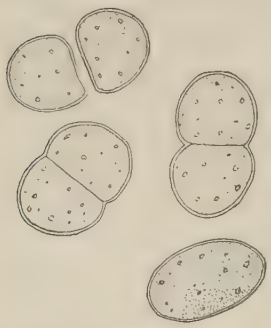


FIG. 231.—*Synechococcus*. A blue-green alga the cells of which are solitary except during fission. Several stages of fission are shown as well as a single cell about ready for division.

Habits and Life History of Representatives of the Cyanophyceae.—The simplest members of this group consist of single cells which are generally spherical or oval. Such a form is *Synechococcus* (Fig. 231). When a single *Synechococcus* individual has grown to a certain size, it divides into two cells of equal size and these soon become separated from each other. Thus one individual gives rise to two. The two new individuals grow in size until they in turn undergo division, and thus four new *Synechococcus* plants are formed. This is a form of asexual reproduction called **fission** which is the simplest form of reproduction. It is restricted to unicellular organisms, and is the sole method of repro-

duction employed by the most primitive plants. It consists merely in the division of a single-celled individual into two protoplasts of equal size and these two new individuals, produced by fission, together contain all the materials of the single parent cell. Organisms which reproduce solely by this method, therefore, never die except as the result of shortage of food or water or other unfavorable external conditions. Natural death (death from old age), such as most plants and animals experience, does not take place among these forms. Each of the new unicellular *Synechococcus* plants is able to carry on all the essential life processes.

They generally live either immersed in water or in very moist habitats where they are wet most of the time. Through the surface of the cell the protoplast within absorbs water, inorganic salts, and the gases, carbon dioxide and oxygen. By photosynthesis the protoplast forms carbohydrates which, as in the higher plants, are used in part for respiration and in part for the formation of substances from which new protoplasm can be built up. As we have seen, reproduction also is carried on by each of these solitary unicellular plants.

In some forms, such as *Gloeocapsa*, which are otherwise not much different from *Synechococcus*, the cell wall is thick and gelatinous but of such consistency that after fission the daughter cells are held within the wall of the parent cell. Each of these cells produces in turn a gelatinous coating of its own. Even after the fission of these daughter cells the jelly-like layer derived from the single cell from which they have arisen may remain intact. Thus we find in a mass of *Gloeocapsa* (Fig. 232), groups of two, four, eight, or even more cells, together with single cells which have been released by the disorganization of the mucilaginous matrix. The cells of a group are entirely independent of the other cells of the same group and are just as well able to carry on all the necessary life processes if freed from any connection with the other cells. *Merismopedia* (Fig. 233) is another blue-green alga the cells of which are held together by a gelatinous matrix. In this form, cell divisions take place alternately in two planes which are at right angles to each other. There results a plate or sheet of cells, one cell thick, and these groups, in which the cells are very regularly arranged, may attain considerable size.

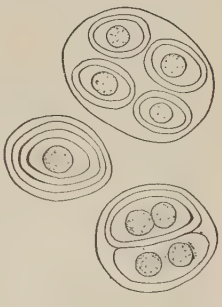


FIG. 232.—*Gloeocapsa*, blue-green alga the cells of which occur generally in groups, the cells formed by the fission of a single cell being held together by the gelatinous coating of the cell from which they came.

In *Nostoc* and *Oscillatoria* the divisions are all in parallel planes, so

that from one cell by a succession of fissions a chain or filament of cells arises. In *Nostoc* many hundred of these filaments are united within a mass of jelly produced by the cells. In some species of *Nostoc* these gelatinous colonies may reach a diameter of 10 or 12 centimeters. Here and there in *Nostoc* filaments, there are enlarged and colorless spherical or barrel-shaped cells called **heterocysts** (Fig. 234). The filaments seem to break apart easily where there is heterocyst, and the resulting short filaments, which are called **hormogonia,** may grow into long filaments by fission of their cells. It is not known of what utility, if any, the heterocysts are to the Cyanophyceae which produce them. Though in *Nostoc* and some other genera they appear to facilitate the formation of hormogonia, there are a number of genera in which the heterocysts are terminal (borne at the ends of the filaments) instead of being intercalary (not at the end), and there are a number of genera which have no heterocysts and yet form hormogonia freely. The hormogonia of *Nostoc* are capable of locomotion and can creep out of the gelatinous matrix and give rise to new colonies. Besides the ordinary oval or spherical vegetative cells, and the heterocysts, a third kind of cell is sometimes found in *Nostoc* filaments (Fig. 234). These are the resting cells, or spores, which are formed from ordinary cells by increase in size, accumulation of reserve food, and thickening of the wall. Their formation is said to be a response to external conditions unfavorable to the vegetative cells. They are probably much more

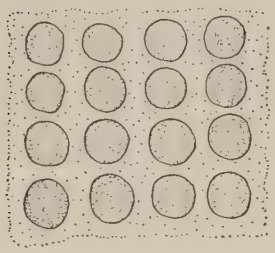


Fig. 233.—*Merismopedia*, a blue-green alga the cells of which are held together by a gelatinous matrix. The cells divide in two planes only and as a result the groups of cells have the form of flat plates. These may grow to considerable size and consist of scores of cells.

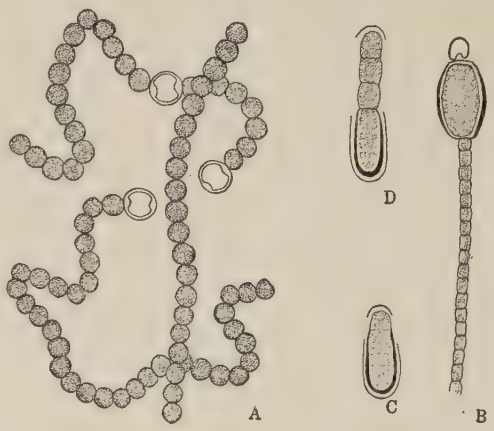


Fig. 234.—*A*, *Nostoc*, filament; *B*, *Cylindrospermum* filament showing heterocyst and thick-walled resting spore; *C* and *D*, germinating resting spores.

resistant to water shortage and unfavorable temperatures than are the ordinary cells. When conditions favorable to the growth of *Nostoc* return, the thick-walled resting cells, or asexual spores, germinate and a new filament is formed.

Another filamentous blue-green alga which is exceedingly common is *Oscillatoria* (Fig. 235). The cells, with the exception of those at the ends of the filament, have the form of short cylinders, which may even be much shorter than they are wide. The terminal cells are generally rounded at the free end, because the turgor of these cells is not balanced by the turgor of an adjacent cell as it is in the case of cells within the filament. The most striking characteristic of *Oscillatoria* is the fact that the filaments are capable of a swaying or oscillating movement, to which the plant owes its name, and of a twisting or rotating motion. In addition, the filaments can move from place to place, so that if a mass of *Oscillatoria* is placed upon a wet surface the threads soon spread out into a uniform film. Neither resting cells or spores are formed in *Oscillatoria*, nor are there any heterocysts. Hormogonia are formed by the death of a cell or of a group of cells, here and there in the filament.

FIG. 235.—A portion of a filament of *Oscillatoria*, one of the commonest blue-green algae. The divisions of the cells take place in parallel planes so that the cell groups are filamentous and unbranched. As the result of the death of a cell here and there, the filament breaks up into short pieces called hormogonia.

Although in *Nostoc* and *Oscillatoria*, the cells are arranged in groups or colonies of definite and characteristic form, and although there may be some differentiation of cells (ordinary vegetative cells, spores, heterocysts), the ordinary cells, if separated from each other without mechanical injury, could doubtless live just as well as isolated cells as they do in the groups. These plants are probably to be considered rather as colonies of unicellular plants than as multicellular individuals, although the distinction between these two states is not a very sharp one.

THE CHLOROPHYCEAE—GREEN ALGAE

Characteristics of the Chlorophyceae.—All of the plants included in this group have chloroplasts and definite nuclei. These two char-

acteristics distinguish the Chlorophyceae from the blue-green algae but not from the red or brown algae.

Most of the green algae possess in their cells only the pigments which are typically present in green cells—**chlorophyll a** and **chlorophyll b, carotin,** and **xanthophyll** (see pages 50 and 51).

The cell walls are not chitinous but are with few exceptions constructed of cellulose. In most of them starch is the first visible product of photosynthesis, although some produce no starch and have oil as the only visible product of photosynthesis.

Distribution of Chlorophyceae.—Members of this group are found in every conceivable moist place where the temperature is not very high and where light can penetrate. The larger number are fresh-water plankton or benthon plants. Relatively few are marine, and most of these occur in tropical seas. There are a number of green algae which are commonly found in soil, but they can live, of course, only very near the surface. A few green algae, such as the common *Protococcus* and *Trentepohlia*, are epiphytes on the bark of trees or attached to fence posts or other objects.

A green alga resembling *Protococcus* is the autophytic component of most lichens, growing in symbiosis with a fungus. There are a few simple green algae which are regularly found in the bodies of certain primitive animals such as the sponges. Some actually live within the cells of animals, as does the alga *Chlorella* in the cells which line the body cavity of the hydra (*Hydra viridis*).

Habits and Life Histories of Representatives of the Chlorophyceae.—We shall not attempt to discuss the various groups of which the Chlorophyceae are made up but shall instead give a brief account of the structure and reproduction of representatives, as follows:

1. Forms which, as far as is known, are without sexual reproduction or zoospore formation—*Protococcus* and *Scenedesmus*.

2. Forms which produce isogametes and zoospores—*Ulothrix*.

3. Forms which produce isogametes but no zoospores—*Spirogyra* and the *Desmids*.

4. Forms which produce heterogametes and zoospores—*Oedogonium* and *Vaucheria*.

Protococcus viridis.—This is a form in which neither sexual reproduction nor zoospore formation is known to occur. *Protococcus* is probably the commonest green alga in the world. It is found everywhere in the temperate parts of both hemispheres except where the climate is very dry. It forms a green coating on rocks, fence posts, and the trunks and branches of trees. This coating is generally restricted to the moister side of branches and fence posts, which in most locations

in the north temperate zone is the north side. Very often this restriction of the growth of *Protococcus* is so well marked that the points of the compass may be approximately determined by observing which side of the tree trunks is green.

The cells of this plant have walls which are quite thick. The protoplast has a definite nucleus with nuclear membrane and a single large distinct chloroplast. This is a lobed structure which partly lines the inside of the cell wall. The large lobes are easily mistaken for separate chloroplasts.

Among *Protococcus* individuals examined under the microscope, there will be found solitary cells which are generally spherical in form,

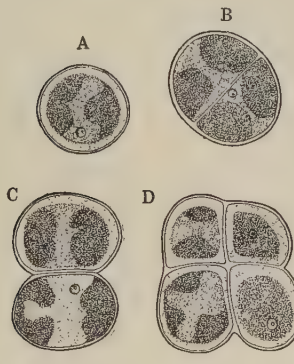


Fig. 236.

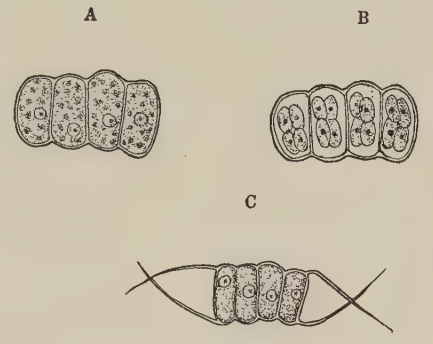


Fig. 237.

Fig. 236.—*Protococcus*, a simple green alga, in which the cells remain united for some time after fission, forming groups of varying size and cell number.

Fig. 237.—*Scenedesmus*, a simple green alga the cells of which form colonies of four (less commonly eight) cells attached side by side. *A* and *C*, two common species. *B*, the first of these giving rise to four new colonies.

groups of two cells, or four cells, and, rarely, of more than four. Where the cells of a group are in contact with one another they are flattened. The groups of two and of four cells arise by successive divisions of one of the solitary spherical cells. The divisions may take place in three planes.

The different cells of the groups eventually become separated from one another, round off, and then undergo division again and form other groups. Reproduction in *Protococcus* is then by fission, and each cell is to be considered as an individual plant, though the separation of the cells of a group is often long delayed.

The cells of *Protococcus* are remarkably resistant to drought. For

a large part of the time they are so dry that the life processes go on at a very low rate. However, when wet by rain or heavy dew they are ready at once to resume photosynthesis and other vital processes.

Ulothrix.—The genus *Ulothrix* is an example of a form having sexual reproduction by isogametes and also asexual reproduction by means of zoospores. It is an unbranched filamentous alga. Some species of the genus grow in fresh water and others in the sea. It is of particular interest because it illustrates how sexual reproduction may have originated. The filaments of *Ulothrix* are made up of short cells, each with a single nucleus and with the single chloroplast in the form of a band around the middle of the cell.

In *Ulothrix* the basal cell of the filament is colorless, elongated and narrowed at the base to form a **holdfast** (Fig. 238, *A*). Here is a simple case of specialization of one cell of a cell group for a function not performed by other cells of the group. In this we have what seems to be the beginning of the development of the multicellular type of plant.

Under certain conditions, not yet well understood, some or all of the cells of the *Ulothrix* filament may give rise to zoospores. The whole protoplast of a cell of a filament may form a single zoospore or it may divide into two, four, or eight protoplasts, each of which becomes a zoospore. In any case there is a contraction and rounding up of the protoplasm and development of four cilia by each zoospore (Fig. 225, *C*). Soon after their formation the spores escape from the filament by a hole which is formed in the lateral wall, and start to swim about in the water. They may continue in active motion for more than an hour and may travel a considerable distance during that time. Finally they cease their movements and attach themselves at the ciliated end to some other alga, to a stone, or to some other object in the water. Following this the cilia are lost and a cell wall is formed, and then by elongation and division the zoospore develops into a new filament (Fig. 238).

Ulothrix reproduces not only asexually by means of zoospores, but sexually by the development of gametes. Gametes are protoplasts which fuse to form the zygote in the process of sexual reproduction. In the most primitive cases of sexual reproduction in plants, the gametes are all alike in size and structure, and are called isogametes. This is the case in the genus *Ulothrix*. Isogametes are generally motile, having cilia, like zoospores. The gametes are, however, usually unable to produce new individuals until they have fused in pairs. It is customary to speak of the fusion of isogametes as conjugation, and of the resulting zygote as a zygospore. The protoplast of the zygospore forms around

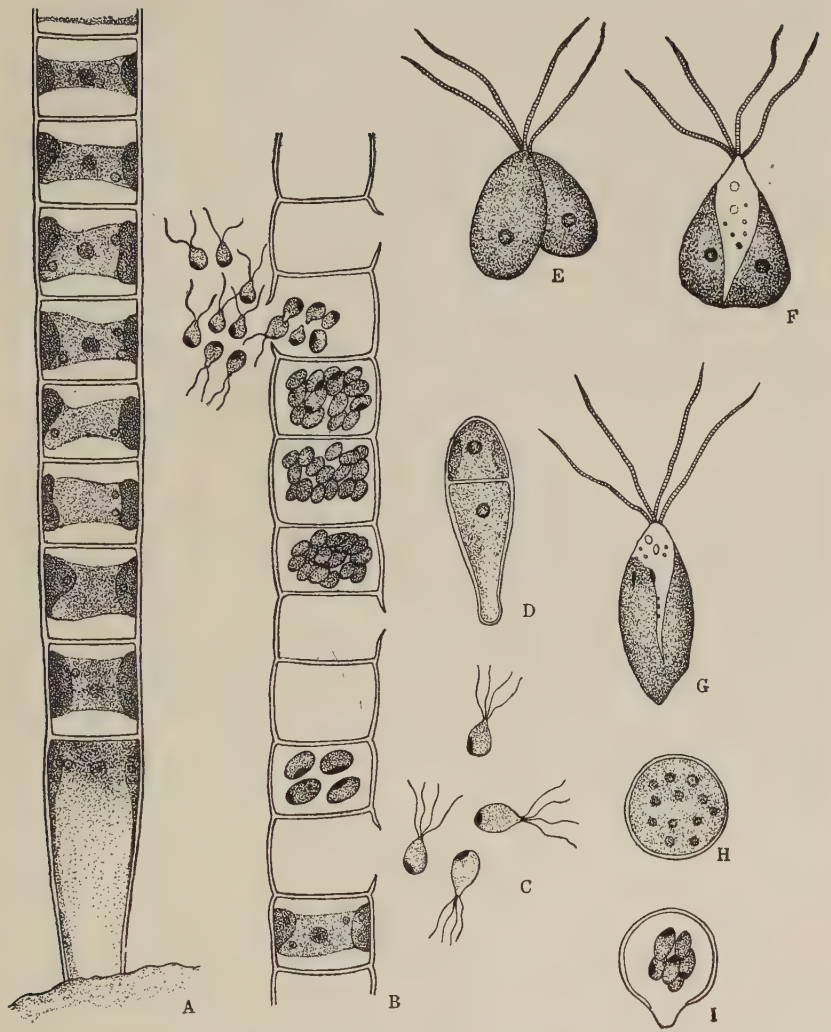


FIG. 238.—*Ulothrix zonata*. *A*, a portion of a filament showing the holdfast cell at the base, and the ordinary vegetative cells. *B*, a portion of a filament which has formed gametes (above) and zoospores (below). These can be distinguished by the fact that gametes bear two cilia each and the zoospores four. *C*, a number of zoospores which have just escaped. *D*, a germinating zoospore. *E*, *F* and *G*, stages in the conjugation of gametes. *H*, a zygospore in the resting condition. *I*, germinating zygospore showing the division of its protoplast into a number of zoospores. (*E*–*H* after Oltmanns.)

itself a cell wall which soon becomes much thickened and protects the protoplast within. The zygospore generally remains in a resting condition for some time before it germinates.

The development of the gametes in *Ulothrix* is very similar to the process of zoospore formation. The gametes arise from divisions of the protoplasts of the cells of the filament, but are generally smaller than the zoospores, a single cell often giving rise to as many as sixteen or thirty-two gametes. Each of the gametes has two cilia instead of four, as in the case of the zoospores. They escape from the cell in the same manner as the zoospores and like them are without any cell wall.

The gametes swim about for a time and then fuse in pairs. The resulting fusion cell, or zygote, secretes a thick wall about itself (Fig. 238). It is called a zygospore since it has been produced by the fusion of similar gametes. Gametes originating in the same filament are said never to fuse, the zygospore being always formed from gametes produced by the different *Ulothrix* filaments.

The zygospores of *Ulothrix* generally remain in a resting condition during the period of the year unfavorable to vegetative activity and later germinate, each producing a number of zoospores which then develop into new individuals.

Under some conditions gametes which fail to fuse may come to rest, round off, and develop a thick wall as do the zygospores. They may later produce new plants in the same manner as the zygospore. Such production of new plants from gametes without fusion is called **parthenogenesis.** It is not of frequent occurrence but it is met with in all the divisions of the Plant Kingdom, even in the Spermatophyta.

The following points in the reproduction of *Ulothrix* are of special significance.

1. Zoospores and gametes are similar in origin and both are naked, motile protoplasts.
2. Zoospores and gametes differ only in size, in the number of cilia, and in the fact that the latter must normally fuse before a new plant can be produced.
3. Zoospores produce new plants at once; zygospores are resistant spores which can withstand unfavorable conditions and normally germinate only after a period of rest.
4. Zygospores do not give rise to new filaments directly, but when they germinate form a number of zoospores which then produce new filaments.
5. Under conditions gametes may without fusion become converted into parthenogenetic spores which, like zygospores, can produce new plants.

Many other algae, some of them not closely related to *Ulothrix*, have gametes and zoospores which are very much alike.

It has been suggested that sexual reproduction may have originated in plants like *Ulothrix*. Probably zoospores were produced by many plants before the origin of sexual reproduction. Sexual reproduction may have first come about by accidental fusion of zoospores. Certain advantages gained by the plant through such fusions may have resulted in this process becoming established. At any rate, there is good evidence that sexual reproduction originated independently in several different groups of plants.

Sea lettuce, or *Ulva*, is a rather close relative of *Ulothrix*. It is common along the coast in many parts of the world. Its plant body is not filamentous but has the form of a thin sheet of cells attached at one end. *Ulva* resembles *Ulothrix* in the very slight differentiation between zoospores and gametes.

Spirogyra.—In the common alga, *Spirogyra* (Fig. 239), we have a representative of a group of algae which produces no zoospores and whose sexual reproduction is isogamous that is, by isogametes. This plant grows only in fresh water and is generally free-floating. The filaments of *Spirogyra* are surrounded by a layer of mucilage which can sometimes be seen under favorable illumination and which gives a characteristic slimy feel to the plant by which it and closely related forms can be easily recognized in the field.

The most characteristic feature of *Spirogyra* is the spirally arranged ribbon-like chloroplast. Certain species have but one chloroplast in a cell while others have several chloroplasts and some may have as many as fourteen. The chloroplast commonly has a lobed or toothed margin. Here and there along the middle of the chloroplasts are conspicuous pyrenoids which are connected by a ridge on the inner side of the chlorophyll band.

The *Spirogyra* cell is cylindrical in form and is lined by a thin layer of cytoplasm in which the chloroplast or chloroplasts are embedded. The nucleus with the cytoplasm which surrounds it is suspended in the center of the single large vacuole, either by fine strands of cytoplasm or by a narrow band of cytoplasm.

The *Spirogyra* filament grows by the elongation and division of all the cells in the filament. Division generally takes place at night. The nucleus divides by mitosis, and then the two-nucleate protoplast is cut in two by a ring of cellulose which grows inward from the outer wall and which finally becomes a disc separating the two new cells.

Reproduction.—No zoospores or other non-sexual spores are produced by *Spirogyra*. However, in some species of *Spirogyra* the cells of the

filaments may become separated from one another and each may grow into a new filament. This suggests the hormogonia of *Oscillatoria* and other filamentous Cyanophyceae.

In *Spirogrya* the gametes are the protoplasts of ordinary vegetative cells. In most cases conjugation takes place between the cells of two

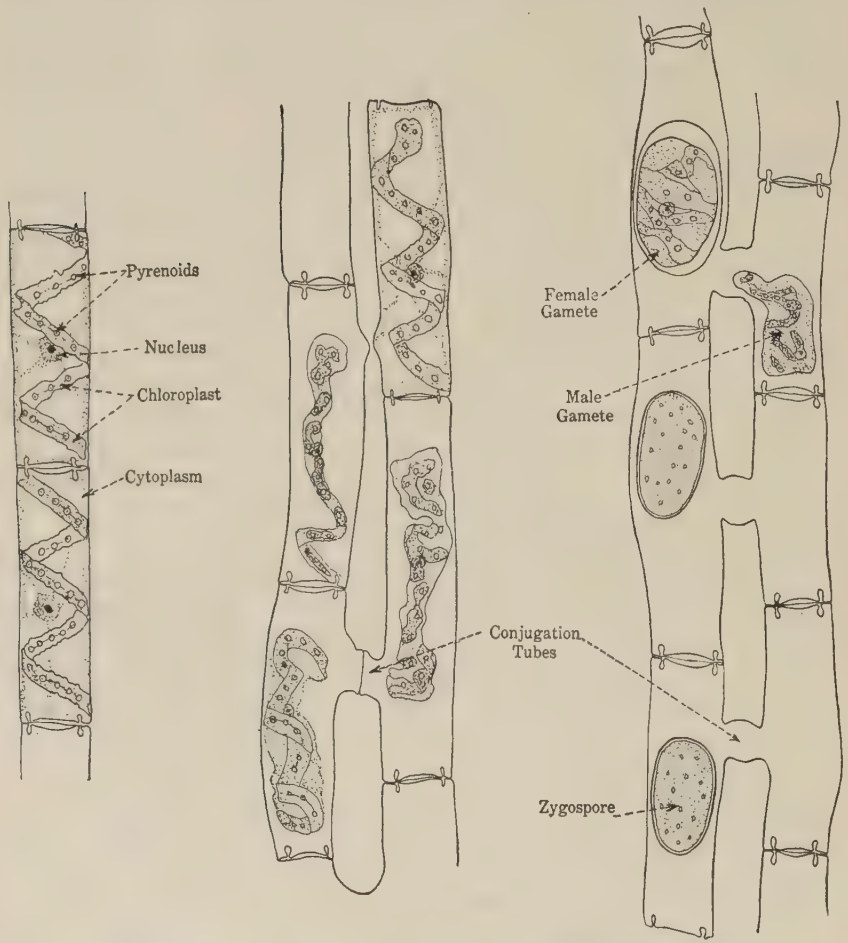


FIG. 239.—*Spirogyra*. To the left two cells from a filament in the vegetative condition. The other two figures show successive stages in scalariform conjugation.

different filaments. This is called **scalariform conjugation** (Fig. 239). Conjugation may also take place between adjacent cells of the same filament. This is known as **lateral conjugation** (Fig. 240). In the

former type of conjugation, tubular outgrowths are produced on the adjacent sides of the cells of filaments which are in contact with each other. The outgrowths from cells which lie opposite one another in the two filaments become attached at the ends and as these outgrowths elongate the filaments are pushed apart. Finally the walls separating the extensions of the conjugating cells are dissolved away and the cell cavities then communicate with each other through the **conjugating tubes.** Meanwhile, the protoplasts which are to fuse contract somewhat. Then the protoplasts (gametes) from one filament pass over into the cells of the other filament and fusion takes place. Though the gametes are morphologically alike and therefore are considered isogametes, the fact that those in one filament remain passive and those in the other are capable of movement indicates a slight physiological differentiation of gametes. In certain species of the genus *Zygnema*, which is closely related to *Spirogyra*, both gametes pass into the conjugating tube and conjugate there. In this case, the gametes show no trace of sexual differentiation.

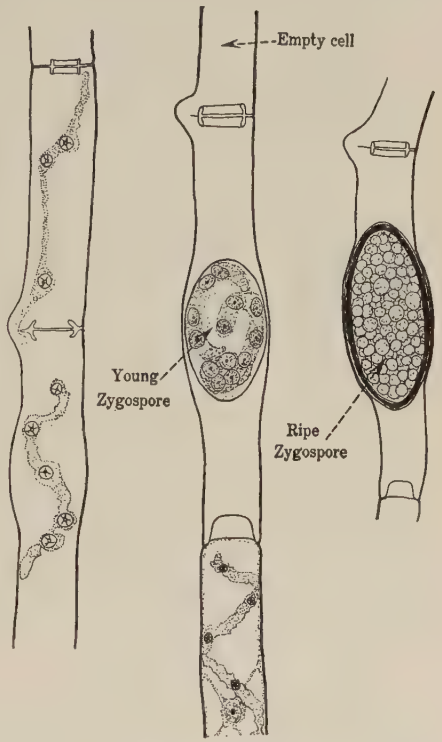


FIG. 240.—*Spirogyra*, showing three stages in lateral conjugation.

In lateral conjugation of *Spirogyra*, a passage is formed between adjoining cells of a filament and alternate protoplasts pass into their neighboring cells. If all the cells of a filament have conjugated by the lateral method, every other cell of the filament is empty after conjugation and alternate cells contain zygotes. However, when all the cells of two filaments conjugate by the scalariform method one filament becomes empty and every cell of the other filament contains a zygote except in cases in which the filaments are of an unequal number of cells. In either case the zygote forms a thick wall which consists of three layers, the outermost and innermost of cellulose and the middle one of chitinous nature. The zygospore when first formed contains abundant starch

which is soon converted into oil. This serves as the food reserve of the spore. The zygospore is highly resistant to extreme cold and to drought. It generally falls to the bottom of the pond or stream where it is formed and, after a period of rest, germinates. Germination is dependent upon conditions favorable for the vegetative activities of *Spirogyra*, that is, abundance of water, moderate temperature, and sufficient illumination. When the zygospore germinates (Fig. 241) it absorbs water, and the protoplast within increases in size and bursts the outer and middle wall of the spore; the inner cellulose wall becomes extended as the protoplast pushes out. At germination the oil of the spore is transformed into starch again. The protoplast of the germinating zygospore forms a tube which elongates and develops into a new filament. The single nucleus of the zygospore contains chromatin derived from the male and female gametes, and thus has twice as many chromosomes as the nuclei of the vegetative cells. It soon undergoes division and the resulting daughter nuclei again divide, so that the zygote has four nuclei. Three of these nuclei disintegrate, so that the mature zygote has but a single nucleus. One of the early nuclear divisions is a **reduction division,** in which the chromosome number is reduced to the normal number for ordinary cells of the species (Fig. 242).

FIG. 241. — Germination of a zygospore of *Spirogyra*.

Desmids.—Belonging to the same order as *Spirogyra* is a group of

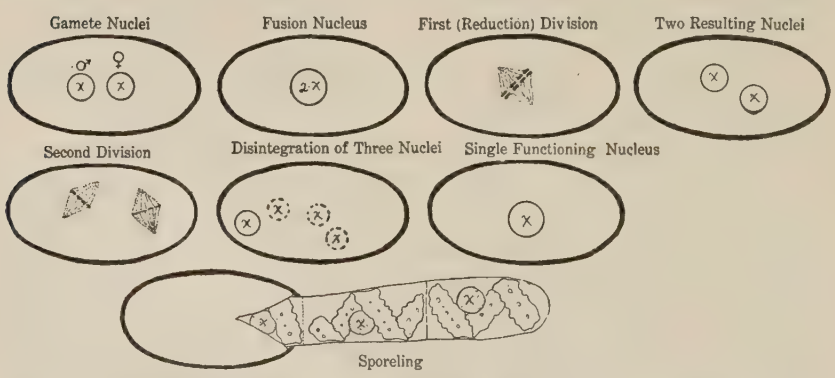


FIG. 242.—Diagrams showing nuclear changes in the zygospore of *Spirogyra* from conjugation to germination.

beautiful unicellular plants, called *Desmids*. For the most part these grow solitary, but sometimes they remain loosely attached after division, and thus come to form filamentous colonies. Some species are common in the fresh-water plankton. One of the most familiar is the crescent-shaped *Closterium*, which is frequently found among filamentous green algae. The most striking feature of this genus is the presence of a small

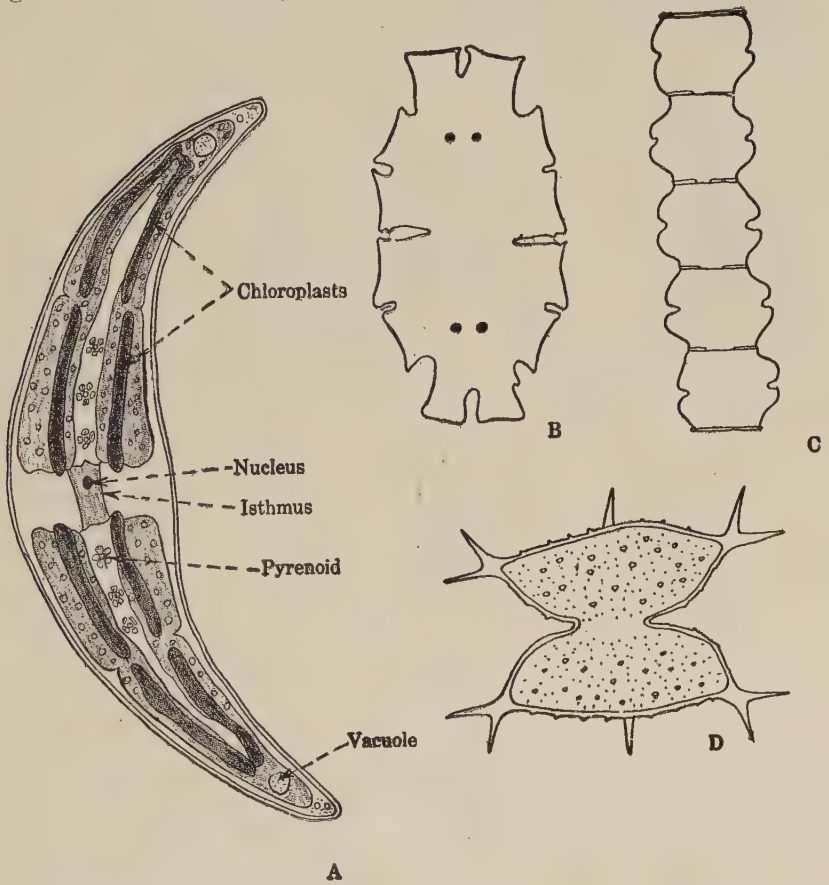


FIG. 243.—Desmids. *A*, *Closterium*, showing the cell contents. *B*, and *D*, two other forms showing the two semi-cells and the constriction (the isthmus) between the semi-cells, two features which are characteristic of most desmids. *C*, desmids united in a filament or chain.

spherical vacuole at each of the extremities of the cells. Within each of these vacuoles is a group of minute crystals of calcium sulphate or gypsum which are in constant vibration. The movement of these crystals is not a vital phenomenon but is the so-called Brownian move-

ment, which can be observed when any very finely divided insoluble substance suspended in water is examined under the microscope. It results from the vibration of the molecules of the surrounding liquid. These molecules are constantly moving and when they strike against one another they rebound. Some of them strike against the suspended particles and tend to displace them, but since the molecular bombardment is from all sides, suspended particles are not caused to move except when they are of very small size. Then, as in the case of these gypsum crystals, a larger number of impacts on one side than on the other will cause a light particle to be displaced, only to be pushed in another direction in the next instant. These vibrating crystals are absent from most desmids.

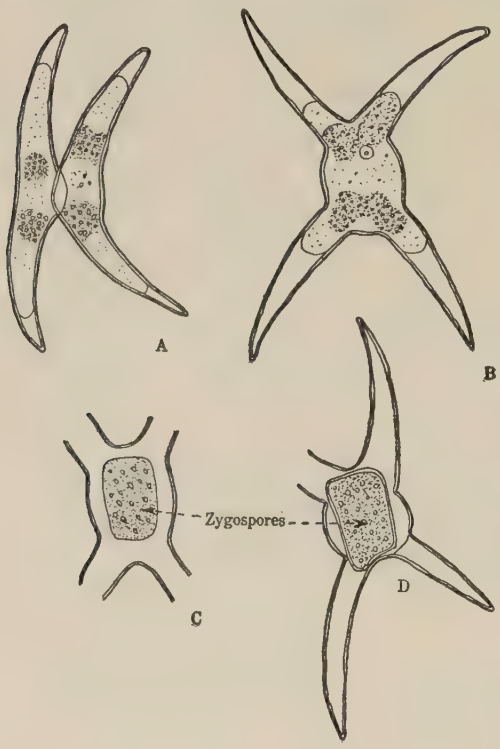


Fig. 244.—Successive stages in conjugation of a species of *Closterium*.

The desmid cell usually consists of two similar halves **semi-cells,** in each of which there is a single chloroplast consisting of six radiating plates Desmids generally have a constriction, called the **isthmus,** between the two semi-cells. Multiplication results from the division of the desmid into two cells, each consisting of one of the previous semi-cells. Then each of these halves develops another semi-cell.

Zygospores are also produced by desmids (Fig. 244). Previous to the formation of zygospores the desmids come together in pairs; then the cell wall of each breaks at the middle line, and the protoplasts escape, those of each pair of desmids fusing. A thick wall is then formed about the resulting zygospore, which, after a resting period germinates to form two new desmids. This is clearly not a method of multiplication, for from two desmids one zygospore is produced and

this in turn gives rise to only two desmids. Zygospore formation is probably of advantage in tiding the plant over a period unfavorable to the existence of the ordinary cells. It is also not unlikely that the mingling of protoplasm from two plants may result in increased vigor.

Oedogonium.—Oedogonium is a common green alga which reproduces by means of zoospores and also by **heterogametes** (unlike gametes). It is a plant with more differentiation among its cells than any form thus far discussed. The basal cell of the filament forms an organ of attachment, or **holdfast** (Fig. 246). Not all the cells in the filament are able to divide and thus add to the length of the filament; certain cells alone

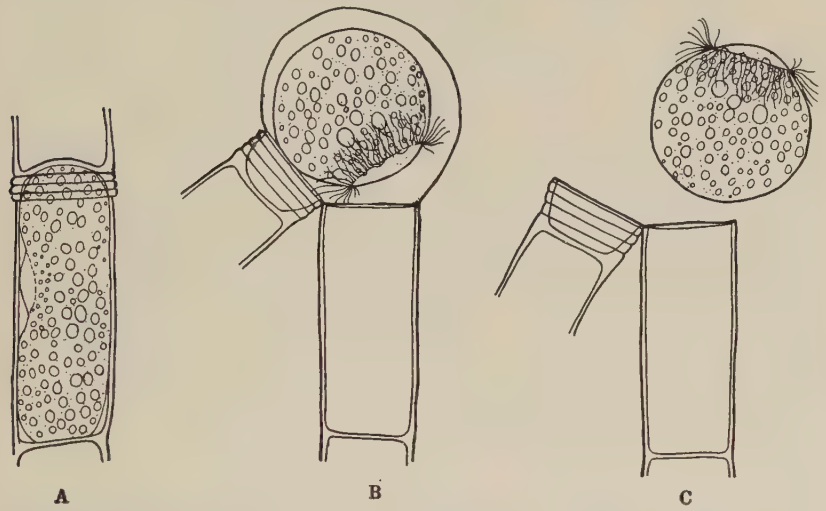


Fig. 245.—Formation and escape of a zoospore in a species of *Oedogonium*. (Redrawn from Hirn.)

have this power. Gametes are not produced in ordinary vegetative cells, as in *Ulothrix* and *Spirogyra*, but in special organs called **gametangia,** much different in form from the vegetative cells although developed from them. On account of this considerable physiological division of labor, *Oedogonium* may well be considered a multicellular plant.

The vegetative cells of *Oedogonium* contain a single nucleus and a chloroplast. The chloroplast differs somewhat in form in different species but it is generally reticulate. The zoospores produced by *Oedogonium* consist of the entire protoplast of a vegetative cell. They are provided with a ring or collar of cilia around the colorless forward end. Generally only a few cells of a filament produce these motile spores. Following its escape from the cell in which it is formed (Fig. 245), the

zoospore swims about for some time and finally comes to rest in contact with some solid object, attaches itself by the ciliated end, loses its cilia, and forms a cellulose wall. It then elongates somewhat and by cell division develops into a new filament. The basal cell remains colorless and develops at the lower end a disc-like or branched holdfast.

Sexual Reproduction.—The male gametes, or sperms, of *Oedogonium* are much smaller than the female gametes, or eggs. The latter are without cilia and remain within the female **gametangium** or **oogonium** until after fertilization. The sperms are like miniature zoospores in form and are produced in much larger numbers than the egg cells. In some species of *Oedogonium* the male gametangia or **antheridia** are produced in the same filament as the oogonia. Such species are said to be **monoecious.** Those species in which the two kinds of gametangia are borne on different filaments are **dioecious.** In either case the oogonia are spherical or oval cells. After the development of the egg a pore is formed, by the dissolution of a small area of the oogonium wall, through which the sperm may enter. The oogonia develop from cells which are at first similar in their appearance to the ordinary vegetative cells. When the oogonium has been formed, the protoplast within shrinks away from the wall and a portion of the egg cell near the pore becomes clear and free from chlorophyll. This is the receptive spot where fusion with the sperm takes place. The sperms are liberated from the antheridia, where they are produced in twos or fours.

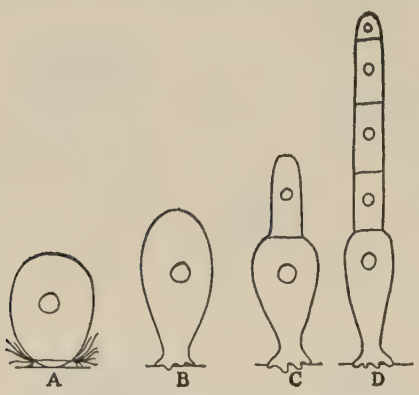


FIG. 246.—Germination of a zoospore of *Oedogonium*, diagrammatically represented.

Fertilization.—Almost immediately after the entrance of the sperm into the egg cell, a thick wall is formed about the zygote or oospore. The contents lose their chlorophyll, and the starch in the zygote is converted into oil. Decay of the oogonium wall releases the oospore, which is resistant to conditions unfavorable to the vegetative cells. It should be borne in mind that the oospore nucleus contains the chromatin from two nuclei and that when it undergoes mitosis, twice as many chromosomes will appear as are characteristic of the nuclei of the vegetative cells. In all plants having sexual reproduction there is such a doubling of the chromosome number when the zygote is formed.

Germination of the Oospore.—After a period of rest the oospore will germinate if the conditions of moisture, temperature, and illumination are favorable (Fig. 248). The spore absorbs water, its wall softens, and the protoplast within increases in size. Then the nucleus divides twice in succession and four protoplasts are formed. Each of these produces a ring of cilia and becomes a zoospore. Thus from each oospore four

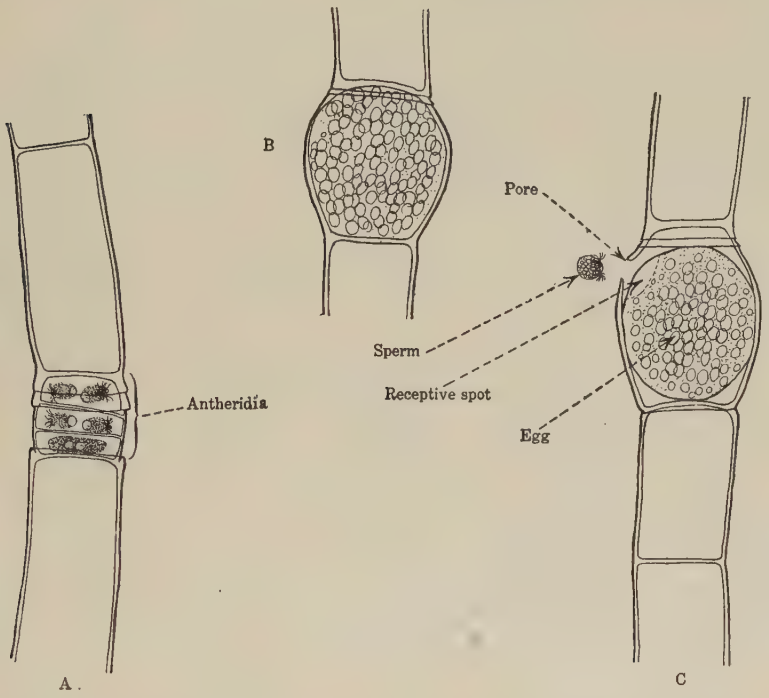


Fig. 247.—*Oedogonium*. *A*, portion of a male filament showing several antheridia. *B*, an immature oogonium. *C*, part of a female filament showing a ripe oogonium, the egg cell of which is about to be fertilized. For the ripe oospore and the structure of a vegetative cell, see Fig. 249, *A*. *C* somewhat diagrammatic.

new individuals may arise. It should be noted that one of the two divisions which result in the formation of the four zoospores is a reduction division and the resulting nuclei have half the number of chromosomes which appear at the first division of the zygote nucleus.

Production of Dwarf Males.—In certain dioecious species of *Oedogonium* the individuals that produce the antheridia consist of very short and narrow filaments, generally of only two to four cells. These are

called dwarf males. They are attached to the female plants and thus grow epiphytically. They arise from special zoospores which are smaller than those which give rise to the female filaments, and are formed in special sporangia, called **androsporangia** (Fig. 249) which are similar in form to the antheridia. These dwarf males are generally found in considerable numbers attached to the outside of the oogonium or to adjacent cells of the female filament.

Significant facts relative to the structure and life history of Oedogonium:

1. The gametes are heterogametes and very different from each other. The female gametes are large, non-motile, well stored with food, relatively few in numbers as compared with the sperms, and are retained within the oogonium until after fertilization.

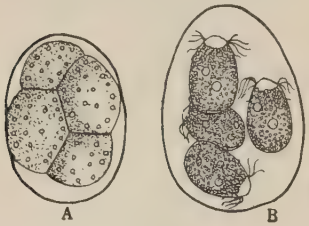


Fig. 248.

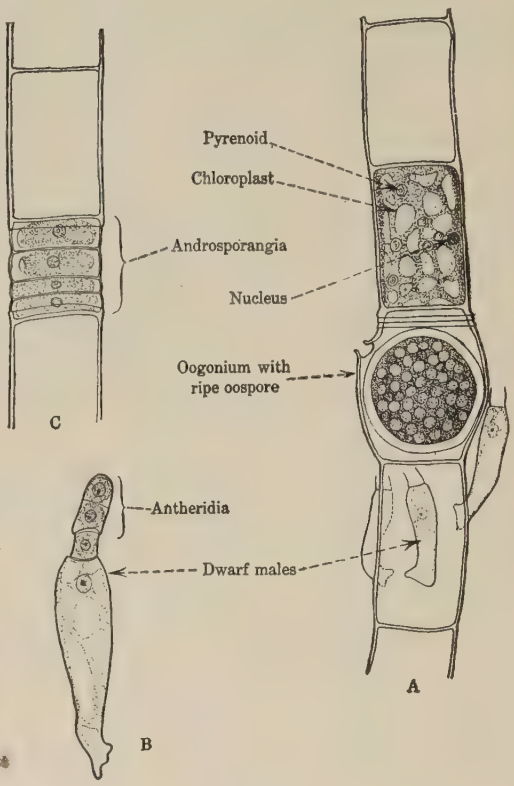


Fig. 249.

Fig. 248.—Germination of oospore of *Oedogonium*. *A*, the protoplast of the oospore dividing into four protoplasts. *B*, the four zoospores formed from the four protoplasts. The oospore has a nucleus with "$2x$" chromosomes, the zoospores having nuclei with "x" chromosomes.

Fig. 249.—A species of *Oedogonium* which produces dwarf males. *A*, portion of an oogonial filament showing the structure of a vegetative cell, an oogonium containing a ripe oospore and three dwarf males which have discharged their sperms. *B*, a single dwarf male showing the holdfast cell at the base and the antheridia. *C*, a portion of a filament with androsporangia within which are developing androspores (zoospores which germinate and give rise to dwarf males).

2. The cells of the filaments are not alike as in *Oscillatoria* or *Spirogyra*, but in addition to the ordinary vegetative cells there are special cells which serve as organs of attachment, special cells to which the function of producing new cells is restricted, and cells which develop into specialized gametangia (antheridia and oogonia).

3. The zoospores and sperms are multiciliate and have the same form, another indication of the correctness of the hypothesis that gametes originated from zoospores.

4. As usual, the zoospores germinate at once and serve as a means of multiplication and distribution, while the oospores, like the zygospores of *Ulothrix* and *Spirogyra* are resting cells which can resist unfavorable conditions. They are a means of tiding the plant over periods unfavorable to growth and food-making, rather than a means of multiplication and dispersal.

5. The oospore at germination produces four zoospores each of which may develop into a new *Oedogonium* plant. One of the two nuclear divisions which result in the formation of the nuclei of these four zoospores is a reduction division.

Vaucheria.—Another very common alga, similar to *Oedogonium* in that it produces heterogametes and reproduces asexually by zoospores, is the so-called "water felt," *Vaucheria*. In the structure of the plant body and of the gametangia and zoospores it is very different from *Oedogonium*.

Most of the species of *Vaucheria* grow in fresh water or on moist soil, although there are a few marine species. It generally grows attached, forming dense mats of filaments. The plant body consists of a branched tube having no cross walls except those which cut off the parts (zoosporangia and gametangia) within which the zoospores and gametes are produced.

The tubular filament is lined with a continuous layer of cytoplasm in which there are embedded numerous nuclei. Plants like *Vaucheria*, whose protoplasm is continuous and multinucleate and without any division by walls into distinct protoplasts, are called **coenocytes.**

In the cytoplasm of *Vaucheria* there are numerous small chloroplasts which, however, are without pyrenoids. Starch is lacking in *Vaucheria*, oil being the first visible product of photosynthesis. Small drops of oil are abundant in the cytoplasm. A large central vacuole runs through the length of the filament. The filaments of *Vaucheria* are relatively weak and easily crushed on account of the absence of cross walls.

Zoospore Formation.—The zoospores of *Vaucheria* are produced at the tips of the filaments, in zoosporangia (Fig. 250) which are cut off by transverse walls from the rest of the filament. The protoplasm of

the zoosporangium contracts from the wall and produces a great number of cilia which arise in pairs. There is a nucleus near the base of each pair of cilia and not far below the surface of the zoospore. The center of the zoospore is occupied by a single large vacuole. *Vaucheria* is unusual in that it produces a coenocytic zoospore. The zoospores of all other genera closely related to it, are relatively small, biciliate protoplasts with a single nucleus and are produced in large numbers in a single zoosporangium. It seems likely that the zoospore of *Vaucheria* is merely the undivided contents of a single zoosporangium.

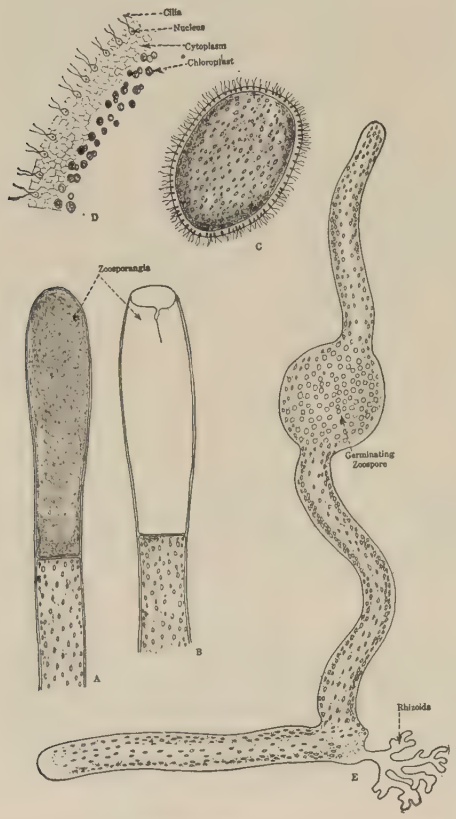


FIG. 250.—Asexual reproduction of *Vaucheria sessile*. *A*, zoosporangium the contents of which will develop into a zoospore. *B*, zoosporangium from which the zoospore has escaped. *C*, a zoospore. *D*, a portion of the peripheral zone of a zoospore. *E*, young plant developing from germinating zoospore. (Redrawn, *A*, *B*, after Gotz; *C*, after Strasburger; *D*, after Sachs; *E*, after Oltmanns.)

This compound zoospore is large enough to be visible to the naked eye. It escapes by the rupture of the end of the sporangium, and after swimming about for a relatively short period germinates by sending out one or more tubes which develop into typical *Vaucheria* filaments. A much branched, colorless organ of attachment may be developed by the filament where it comes in contact with some solid object.

Sexual Reproduction.—The oogonia and antheridia are produced from short side branches of a vegetative filament. In some species several antheridia and oogonia are produced at the end of a special green branch.

The antheridium is an elongated curved structure. The multinucleate protoplasm of the antheridium is cut off by a transverse wall from the protoplasm of the vegetative part of the plant. From the protoplasm of the antheridium there develop a number of sperms, one

for each nucleus. These male gametes are pear-shaped and have two cilia which are attached laterally. They escape by the dissolution of the end wall of the antheridium.

The protoplasm of the oval oogonial branch is at first multinucleate, but before the oogonium is cut off from the rest of the plant all the nuclei except one either return to the filament or, as some investigators have reported, undergo degeneration within the oogonial branch. After the formation of the wall which separates it from the main filament, the contents of the oogonium contract. A beak is formed at the end of the oogonium and through this an opening is formed by which the sperm may enter to fertilize the egg cell.

After fertilization the oospore forms a thick wall and undergoes a resting period. Upon germination it produces a new filament directly, without zoospore formation.

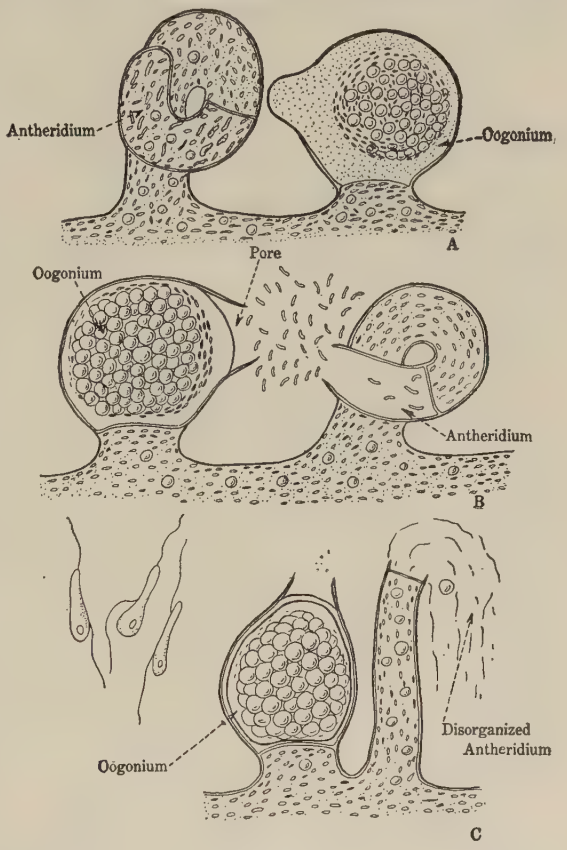


FIG. 251.—Sexual reproduction in *Vaucheria sessilis*. *A*, gametangia before fertilization. The antheridium not yet mature, the oogonium mature and ready for fertilization. Note the cytoplasm of the egg protruding through the pore. *B*, just after the escape of the sperms and the fertilization of the egg. *C*, some time after fertilization, showing the thick-walled oospore within the oogonium and the disorganized antheridium. To the left of *C*, several sperms. (Redrawn after Sachs.)

Other Green Algae.—Systematic botanists have divided the Chlorophyceae into a number of smaller groups, each of which seems to have evolved independently from some ancestors belonging to a single group of simple organisms, probably the Flagellates. Within several

of these smaller groups it is possible to find series of genera which indicate the development from very simple forms without sexual reproduction, through forms of more complexity and with isogamous sexual reproduction, to larger and still more complex forms in which the gametes are highly differentiated. It appears that among these plants there has been, at least in several of the smaller groups, a parallel development from very simple to more complex plant bodies, and that sexual reproduction and the development of heterogamy has taken place independently.

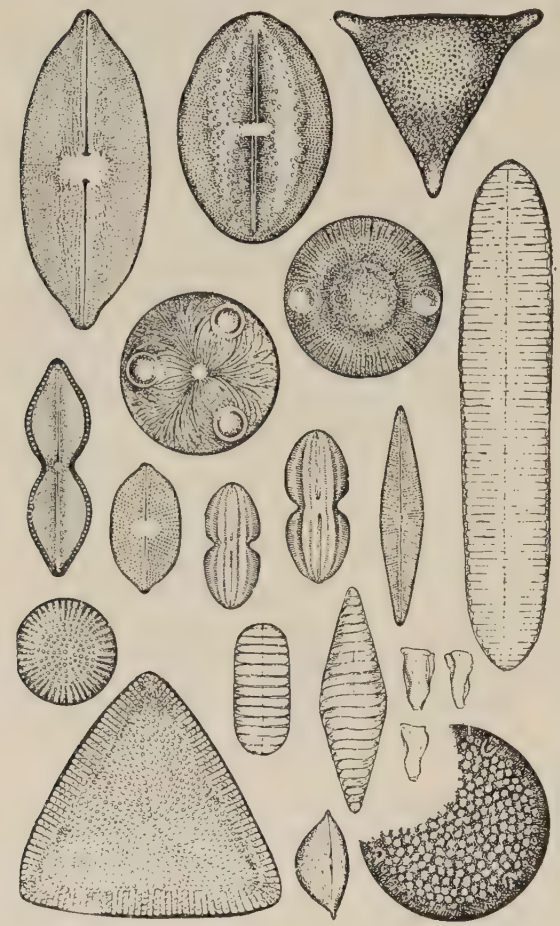


Fig. 252.—Diatoms (all highly magnified) showing various forms and markings. (From Wolle's *Diatomaceae of North America.*)

There are many beautiful and interesting green algae which it has not been possible to describe. A number of them are shown in the accompanying figures. One group of unicellular plants which are considered by some to be related to the Phaeophyceae and by others to belong rather with the Chlorophyceae deserve inclusion in our discussion. These are the **diatoms** (Fig. 252). Their most striking characteristics are the large quantity of silica with which the cell wall is impregnated and the fact that the wall consists of two halves, called **valves** (Fig. 253) which fit together like the two parts of a pill box. These minute plants sometimes form colonies, but most species are truly unicellular and are found either attached to larger water plants or

other objects or floating free in the water. They are a very important component of the plankton of the sea and of lakes and ponds. Some two thousand species of diatoms have been described.

The protoplast enclosed within the valves of the cell wall contains a single nucleus and generally two chloroplasts. In addition to chlorophyll, an accessory pigment, brown in color, is present in most cases. When floating marine or fresh-water diatoms die, and the cellulose of the wall is decomposed, the form of the valves and the delicate sculpturing characteristic of the valves of many species remain intact because of the large quantity of silica present. These dead diatoms sink to the bottom and accumulate in great quantities. In some regions which were once below the level of the sea, great deposits of these remains (called diatomaceous earth) have been found. In Ehrenberg, Germany, there is a deposit of this kind 4 meters thick, and deposits twelve or fifteen times that thickness exist at several places in the United States. In a cubic centimeter of this material there may be over two and a half million diatom shells. Diatomaceous earth is used as a polishing material and also for mixture with nitroglycerine in the manufacture of certain grades of dynamite.

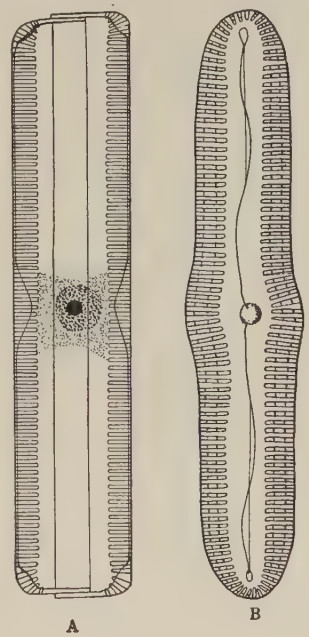


Fig. 253.—Diagrams showing the structure of a diatom (*Navicula*) as seen in two views. The two longitudinally placed ribbon-like chloroplasts are not shown. (Redrawn from Ehrenburg.)

Though most diatoms are autophytic (able to manufacture their own food by photosynthesis) there are a few species, living in water containing much organic matter, which are colorless and live as saprophytes by absorbing their food from the water instead of making it. Many diatoms are capable of rather active locomotion. They multiply by the division of the protoplast into two, each of the protoplasts receiving one of the original valves and forming one new valve. As a result, one of the new diatoms is smaller than the parent cell. Sometimes the protoplasts of two small diatoms escape from the valves and fuse to from a zygote, called an **auxospore,** from which a full-sized diatom develops.

THE PHAEOPHYCEAE

The third class of the algae, brown algae, or Phaeophyceae, includes the largest and the most highly differentiated of the thallophytes as well as many forms of small size and very simple structure. The range of size is from species which are microscopic to such genera as *Macrocystis* which probably may become as much as 200 meters in length, although that figure has never been definitely authenticated. The latter form no doubt exceeds in length any other organism now living.

Characteristics of the Phaeophyceae.—No unicellular organisms are found in this group. All the Phaeophyceae have cells with definite nuclei and distinct plastids. These latter contain, in addition to chlorophyll *a*, chlorophyll *b*, carotin, and xanthophyll, a brown accessory pigment called **fucoxanthin,** which usually entirely hides the green color of the chlorophyll. All of the brown algae grow normally attached but plants may become detached and still survive. Floating masses of the brown alga, *Sargassum* (Fig. 258), make up the greater part of the flora of the Sargasso Sea. In the Phaeophyceae no resting spores are produced. All motile cells, whether zoospores or gametes, have two cilia which are laterally attached.

Distribution of Phaeophyceae.—These plants are much more common and better developed in the cool ocean waters of the temperate zones than in warm tropical seas. Only a few species are ever found growing in fresh water.

Representatives of the Class.—Among the best-known representaties of this class are the simple filamentous species of the genus *Ectocarpus*; the large forms which are called "kelps" and which include the common genera *Laminaria*, *Nereocystis*, *Macrocystis*, and *Postelsia* (sea palm); and the rock weeds (*Fucus*).

Structure and Life History of Ectocarpus.—*Ectocarpus* is a form which, like *Ulothrix*, illustrates the probable origin of sexual reproduction. The plant body consists of attached tufts of branched filaments consisting of one or several rows of cells. The zoosporangia are generally single cells borne at the end of a special short lateral branch, although they may be within the main filament. Numerous zoospores are produced within each sporangium. They escape by the dissolution of the wall at one place and swim about for some time by means of their two unequal, laterally inserted cilia. When they come to rest they develop directly into new individuals.

The gametangia are multicellular structures, larger than the sporangia and generally on a special lateral branch. They are made up of cubical cells, the protoplast of each of which becomes a gamete. The

gametes are similar to zoospores in structure but normally do not develop new plants without fusion to form a zygospore. When the zygospores germinate they give rise to new plants directly.

Among the different species of *Ectocarpus*, there are apparently the beginnings of a differentiation of gametes. In some forms there is a slight difference in size, and it is said that in such cases only gametes

FIG. 254.—Structure and reproduction of a species of *Ectocarpus*. *A*, habit drawing. *B*, portion of a plant showing zoosporangia. *C*, a single gametangium and vegetative cells. *D*, portion of a plant showing gametangia. *E*, two zoospores. *F*, several stages in conjugation, including a zygospore, to the right of the letter. *G*, two gametes about to conjugate. (*A* to *D* after Setchell and Gardner.)

differing in size are able to fuse. In some other species, in addition to size differences, there is also said to be a difference in degree of motility, the larger gametes moving less actively and coming to rest earlier than do the smaller ones which fuse with them after they become quiescent.

In short, little distinction seems to exist in the genus *Ectocarpus* as a

whole, between zoospores and gametes, and there occur various gradations between isogametes and heterogametes.

The Kelps.—These are the plants which form the extensive kelp beds off the Pacific coast. The largest of the kelps, *Macrocystis*, is said to reach a length of 200 meters; and the stalk of *Nereocystis* (Fig. 255)

FIG. 255.—Three young plants of one of the largest kelps (*Nereocystis Luetkeana*). (After Postels and Ruprecht.)

has been known to grow to a length of 30 or 40 meters. These plants possess a **holdfast,** or organ of attachment, which superficially resembles a root system, a stalk or **stipe,** and expanded blade-like portions which strongly suggest the leaves of the Spermatophytes. There is a considerable differentiation of tissues also.

The kelps were formerly believed to be isogamous plants. It has been recently shown, however, in the case of several species, that the

structures formerly thought to be isogametes are really zoospores, and that these upon germination give rise to very small plants quite unlike the typical kelp plants. These minute plants, which have previously escaped discovery, are of two sorts, antheridial and oogonial, producing respectively sperms and eggs. From the zygotes resulting from the fusion of sperms and eggs develop typical kelp plants. Thus there is an alternation of generations in these plants and probably in many of the kelps, a gametophyte phase or gamete producing generation alternating with a generation which produces asexual spores. This is a condition

FIG. 256.—A large kelp (*Pelagophycus*) from the Californian coast. (Photograph furnished by W. A. Setchell.)

which also exists in certain Rhodophyceae and which is the rule in all the Bryophyta, Pteridophyta and Spermatophyta.

Fucus.—*Fucus* (Fig. 260) is the so-called bladder wrack, which is generally abundant on the rocks between the high and low tide levels on the shores of most temperate seas. It is closely related to *Sargassum* (Fig. 258), which is found mostly in tropical seas. Off the southeast coast of the United States is the great area, about a quarter of a million square miles in extent, of floating seaweed called the Sargasso Sea. The principal plants found there are two species of *Sargassum*. Pieces of these plants probably were brought by ocean cur-

rents from the coasts of the West Indies or of tropical America where they grew attached. For ages they have multiplied vegetatively in the Sargasso Sea.

Life History of Fucus.—Since there is no asexual method of reproduction in *Fucus*, it is convenient to begin the life history with the zygote or oospore. This is produced outside of the plant in the open sea by the fusion of one of the very great number of biciliate sperms with a very large egg cell, which may have a volume as much as thirty thousand times as great as that of a sperm.

Fig. 257.—The sea palm (*Postelsia*), a remarkable kelp found on some of the most exposed rocky shores of the California coast, where it is almost constantly subjected to the battering of the waves. This plant has a very effective system of holdfasts and a stout stipe surmounted by flattened blades. (From a photograph furnished by Gardner and Setchell.)

Germination of Oospore.—This zygote does not become a resting spore, as in the fresh-water algae, but almost at once forms a thin cellulose wall about itself and then germinates and grows into a new plant. When it germinates it forms, on the side away from the light, a short tube (Fig. 259). By this tubular outgrowth, which may branch, the new plant attaches itself to some solid object. Shortly after germination begins, the zygote is divided into two cells by a wall which is formed at right angles to the direction from which the light falls upon the oospore. Then many cell divisions take place, so that soon the plant is made up of many cells. One of these, at the extreme tip, is the **apical cell.** It is in a constant state of division and corresponds to the primordial meristem of the seed-bearing plants. After the formation of the apical cell all subsequent growth of the plant results from the division and enlargement of cells cut off from this cell. We shall find that such growth from an apical cell is characteristic of most of the plants belonging to Bryophyta and Pteridophyta, as well as of *Fucus* and some other large marine algae. As cell division and enlargement of the new cells

continues in *Fucus*, the new plant develops a body consisting of (1) a disc-like holdfast, (2) a stalk called the **stipe,** and (3) a broad and flattened part, somewhat resembling a leaf.

By this time it is possible to see at the extreme end of the expanded portions an elongated pit. The apical cell lies at the bottom of this pit. Before the new *Fucus* plant has attained any considerable size, the apical

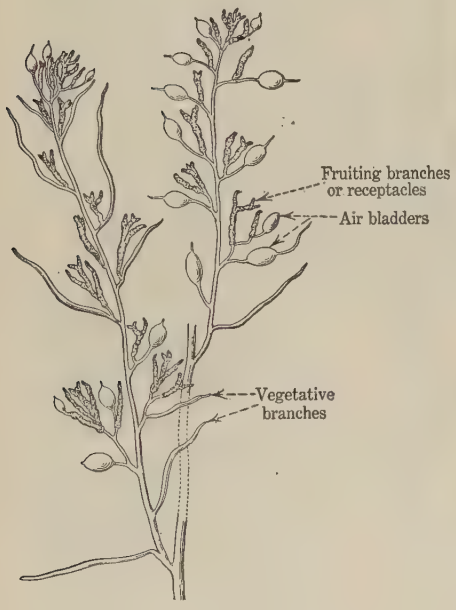


Fig. 258.

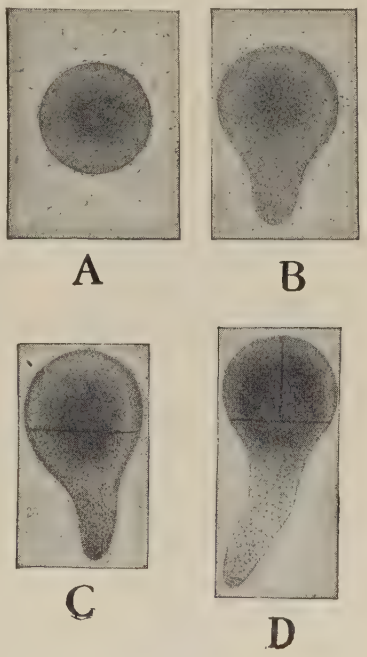


Fig. 259.

Fig. 258.—Part of a plant of *Sargassum.* (After Gardner and Setchell.)

Fig. 259.—Fertilization of the egg and germination of the oospore of a species of *Fucus.* *A,* an egg surrounded by many sperms. *B,* an oospore germinating. The tubular outgrowth, which later forms a holdfast at the tip, arises always on the side of the oospore away from the light. *C,* the young plant has divided into two cells by a transverse wall. *D,* a wall at right angles to the first divides the upper of the cells into two cells. (After Thuret.)

cell divides lengthwise into two equal halves, each of which now functions independently as an apical cell. As a result, a forking of the frond takes place and after a time each of the branches will again fork as a result of the division of each of the apical cells into two. This method of branching by forking is called **dichotomy.** It is relatively rare among plants. Much more common is the monopodial type of branching in

which numerous small branches are given off from a main axis or stem which is continuous.

Structure of the Mature Plant.—A cross section of a vegetative branch of *Fucus* shows a marked differentiation of tissues. There is a compact, dark brown, outer region called the **cortex,** and an almost colorless central portion made up of a loose mass of elongated cells and called the **medulla** (Figs. 261 A and 262 A).

In certain species of *Fucus* (notably *Fucus vesiculosis* of the Atlantic coast) air bladders, which arise by the accumulation of gas in large

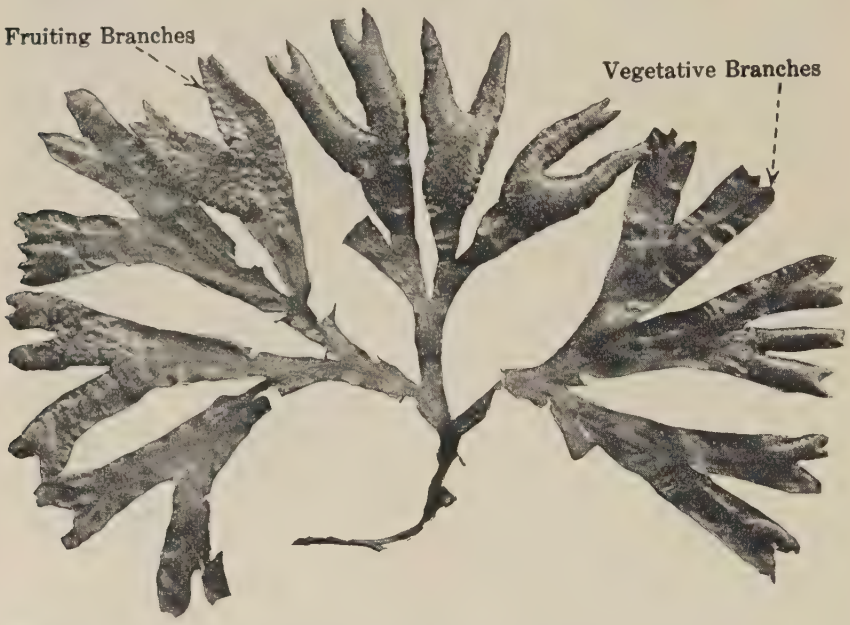


Fig. 260.—A frond of a species of *Fucus*, showing the dichotomous method of branching, vegetative branches, and fruiting branches with numerous conspicuous swellings (openings of the conceptacles). (Photograph furnished by Gardner and Setchell.)

intercellular spaces, are borne some distance from the tips of the flattened branches.

Reproduction.—The gametangia are borne within nearly spherical chambers in the swollen tips of the branches. These cavities are called **conceptacles** (Fig. 261). Each conceptacle opens to the surface of the branch, by a small pore, the **ostiole.** From the inner surface of the conceptacle, slender, multicellular, unbranched hairs (**paraphyses**) grow out. They are all directed toward the ostiole, and in certain species of *Fucus*

some of them actually grow out through the ostiole, and protrude as cottony tufts. Directed as they are toward the opening (ostiole) of the conceptacle, the parphyses probably facilitate the escape of the gametes when the latter become mature, for fertilization in *Fucus* takes place outside the conceptacles.

The common eastern species, *Fucus vesiculosis*, is dioecious. In that species the male branches, when the gametangia are mature, can be easily distinguished from the female branches because of the yellow or orange color imparted to the former by the immense number of sperms, each of which has an orange pigment spot. In other species the plants are monoecious and the antheridia and oogonia are produced within the same conceptacle.

Development of Sperms.—Antheridia are produced among the paraphyses of the antheridia conceptacles of dioecious species or the mixed conceptacles of monoecious species (Fig. 261). They are oval cells which are borne on much-branched hairs. Each of the cells which is to become an antheridium contains at first a single nucleus. This nucleus divides into two, and these into four, and so on until in most species

FIG. 261.—A dioecious species of *Fucus*. *A*, cross section of a fruiting tip of a male plant, showing the compact outer region (the cortex), the loose tissue within (the medulla), and several antheridial conceptacles. *B*, a single antheridial conceptacle in section showing the opening to the surface (the ostiole) and the antheridial-bearing hairs which arise from the inner surface. *C* and *D*, antheridia and the branched hairs upon which they are borne. (After Thuret.)

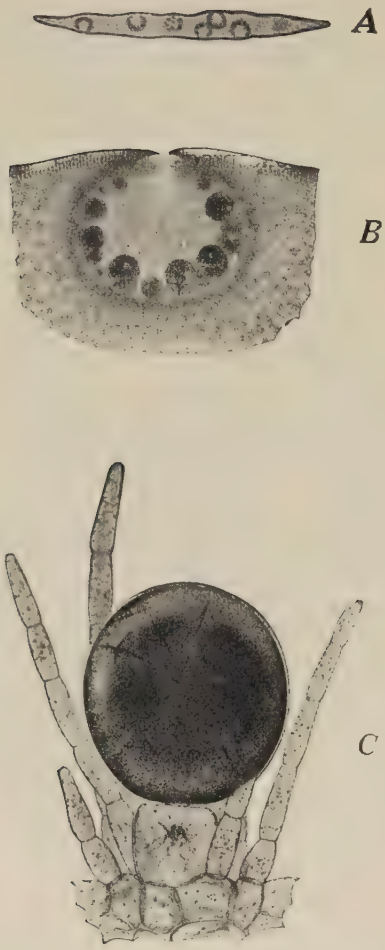


FIG. 262.—A dioecious species of *Fucus*. *A*, a cross section through a fruiting branch of a female plant showing the cortex, medulla, and several oogonial conceptacles. *B*, a single oogonial conceptacle in section, showing the ostiole and the oogonia and paraphyses which line the conceptacle. *C*, a portion of the floor of the conceptacle showing an oogonium attached by its stalk cell and surrounded by a number of paraphyses. Note that the protoplasm of the oogonium has undergone cleavage to form the eight eggs which have not yet rounded up. (After Thuret.)

sixty-four nuclei result. Finally each nucleus, with a small amount of cytoplasm, becomes a sperm. The sperms are more or less pearshaped and have two laterally attached cilia of unequal length and a pigment spot or eye spot. When the sperms are mature the whole mass within one antheridium escapes by a rupture of the outer layer of the antheridium. The paraphyses secrete considerable mucilage. When the *Fucus* plants are exposed to the air between tides, there is some drying out of the fronds and some shrinkage. The contraction of the outer tissue of the fruiting frond results in the mucilage within the conceptacle, together with masses of sperms or eggs, being extruded from the ostiole. The rising tide washes off the extruded mucilage and liberates the gametes which are then free to fuse.

Development of Eggs.—The oogonia are also borne among the paraphyses. In the development of these gametangia a short outgrowth arises from the cells which form the wall of the conceptacle. This outgrowth divides transversely into two cells of which the outer becomes the oogonium and the inner a **stalk cell.** The oogonial cell enlarges and becomes filled with dense protoplasm. Its single nucleus then undergoes three successive divisions, giving rise

to eight nuclei. There follows a division of the cytoplasm into eight masses, each of which with a nucleus becomes an egg (Fig. 262). These eggs become rounded within the oogonium but are without any cell wall.

The oogonium wall is made up of several layers. At maturity of the eggs the outermost layer is ruptured and the eight eggs escape from the oogonium but remain within the two inner layers of the wall. In succession the outer and the inner of these layers ruptures and the eggs are finally allowed to escape into the sea water (Fig. 258, A) where fertilization takes place. The fertilization of many of the eggs is made certain by reason of the great numbers and motility of the sperms and the characteristic substance given out by the egg, which attracts the sperm.

In *Fucus* the reduction of chromosomes, from the double or **diploid** number characteristic of " the plant " to the half or **haploid** number found in the egg and sperm, takes place at the first division of the antheridial and the oogonial cells, that is not long before the time of gamete formation. At fertilization the chromosome number is doubled, so that the oospore and the plant into which it develops have nuclei with the diploid chromosome number.

Among the most important features of the structure and life history of *Fucus* are the following:

1. The great size and complexity of the plant body compared with the Cyanophyceae and the Chlorophyceae, and the considerable differentiation of tissues. These are even more marked in some of the kelps.
2. The terminal growth from a single apical cell.
3. The habit of dichotomous branching.
4. The absence of zoospores or other means of asexual reproduction.
5. The extreme differentiation of the gametes, the sperms being very small in size, highly motile, and produced in very great numbers, and the eggs being large, relatively few in number, and without power of locomotion.
6. The production of a number of egg cells within a single oogonium.
7. The fact that the eggs, instead of being retained and protected within female gametangia until after fertilization, as in *Oedogonium*, and *Vaucheria* and in the Bryophyta and the Pteridophyta, are expelled before fertilization.
8. The fact that the reduction division takes place when the gametes are produced (at the first divisions of the antheridial and oogonial cells) and not, as in *Spirogyra, Oedogonium,* and *Vaucheria,* at the germination of the zygote.
9. The almost immediate germination of the oospore, in contrast with the delayed germination of the zygotes of *Spirogyra, Oedogonium, Ulothrix,* and *Vaucheria,* which are resting spores.

THE RHODOPHYCEAE—RED ALGAE

The fourth class of algae is made up of plants which are mostly marine, although a few species live in fresh water. All the members of this class are multicellular. In general they are clearly more differentiated than the green algae, but as a group are characterized by simpler structure than the kelps and the Fucales. Most of the vegetative cells have a single nucleus, though in some of the red algae large vegetative cells with several nuclei occur. The plastids, which may occur in large numbers in each cell, contain in addition to chlorophyll *a*, chlorophyll *b*, carotin, and xanthophyll, an accessory pigment called **phycoerythrin.** True starch is never found in the Rhodophyceae, but grains of a reserve carbohydrate, which stains red instead of blue when treated with iodine, are often present.

FIG. 263.—A portion of a plant of *Pterosiphonia*, a genus closely related to *Polysiphonia*. The tetrasporic plants, the male plants and the female plants can not be distinguished by the naked eye. (Photograph furnished by N. L. Gardner.)

In many red algae the cell walls are very thick, so that the protoplasts appear to be embedded in an extensive gelatinous matrix. In these forms there are often pits in the cell walls through which extend protoplasmic connections between the protoplasts of adjoining cells. Some of these plants, which have a finely branched plant body, are certainly to be considered the most delicate and beautiful of all marine plants. In one group of red algae, the coralline algae, the cell walls become encrusted with large quantities of carbonate of lime and are strongly suggestive of corals. Certain related red algae similarly encrusted with lime have played an important part in the building up of coral reefs. No ciliated cells have been found in the red algae. Sexual reproduction is always heterogamous.

Distribution.—The Rhodophyceae are abundant in the temperate seas, but the number and variety of forms are greater in the warmer

tropical and sub-tropical waters. They are generally found below low-tide level and may grow at depths as great as 200 meters.

Function of Accessory Pigment.—The production of a red pigment by these algae is said to be an adaptation to their life in relatively deep waters. Since the light, which has passed through water of some depth, has had the rays of the red end of the spectrum largely absorbed, it is important that a large part of the rest of the light should be absorbed by the plant. The pigment of these deep-living Rhodophyceae is such as to bring about more complete absorption than would a green pigment alone.

Reproduction.—None of the red algae produce ciliated cells of any kind. Sexual reproduction is in all cases heterogamous. The male gametes are spherical, non-motile **sperms** which are carried by the movements of the water to the female gametangia, or **carpogonia.** Each carpogonium is a cell enlarged at the base and elongated at the upper end into a long filament, the **trichogyne** and when a spermatium comes into contact with a trichogyne it is held there. Then the wall of the trichogyne dissolves at the point of contact and the nucleus of the male gamete passes down the trichogyne and fuses with the nucleus of the female gamete at the base of the trichogyne. Instead of forming a single oospore, the zygote gives rise to numerous short branches on the ends of which are borne spores called **carpospores.** In some species the formation of these carpospores from the zygote is a process of great complexity.

The sexual reproduction of the Rhodophyceae is of particular interest because a very similar process has been found to take place in certain fungi.

Alternation of Generations in the Rhodophyceae.—In some of the simpler red algae the carpospores germinate and produce new plants upon which are produced carpogonia and spermatia. These are, however, the exceptional cases. In a number of other members of this group, for instance the genus *Polysiphonia*, the life history is more complicated. In these forms, when the carpospores germinate they give rise to plants which resemble superficially the plants that produce carpogonia and spermatia, but which never form gametes. Instead of gametes, these plants which develop from the carpospores form asexual spores, called **tetraspores.** These spores are produced in groups of four, each group resulting from two successive divisions of certain cells of the asexual or tetrasporic plants. The tetraspores upon germination never give rise to tetrapsoric plants but instead to sexual plants bearing spermatia and carpogonia. Thus the life cycle consists of two phases which alternate with each other.

It has been shown that, in *Polysiphonia* and in several other genera in which this alternation of asexual and sexual phases or generations takes place, the sexual and asexual plants are characterized by a dif-

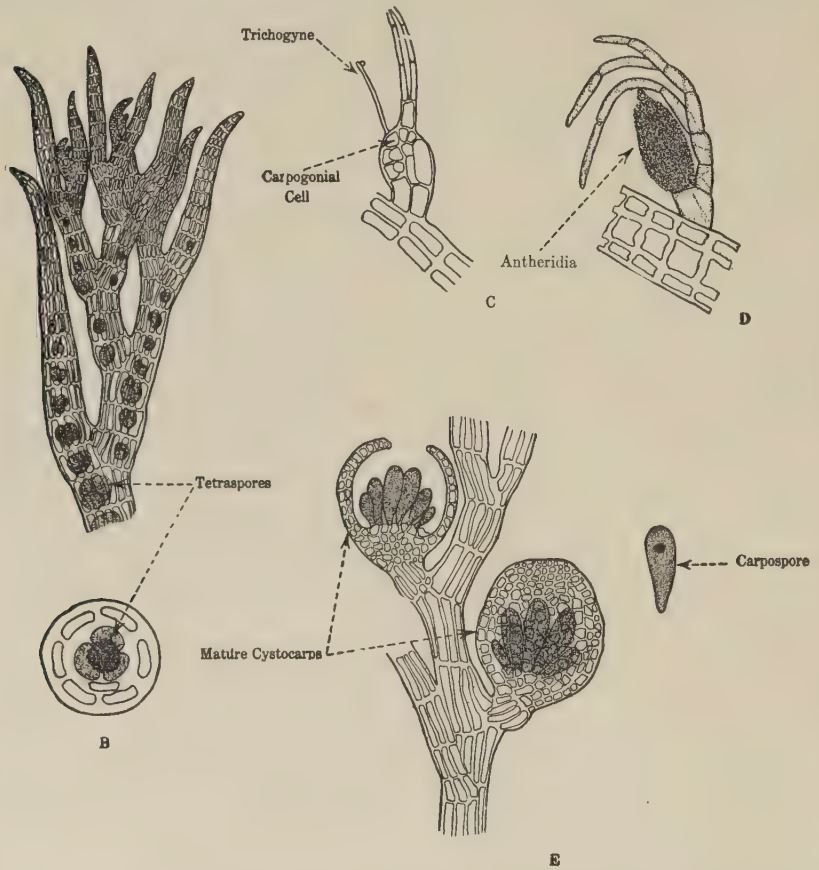
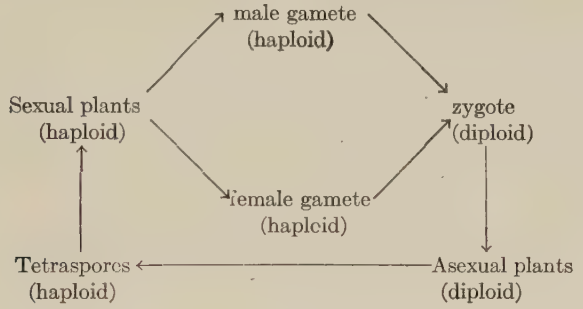


FIG. 264.—Structure and life history of a species of *Polysiphonia*. Upper left, a fragment of a tetrasporic plant, showing the form and arrangement of the vegetative cells (this feature is the same in the sexual plants), and groups of tetraspores. *B*, cross section of a branch showing the arrangement of the tetraspores and vegetative cells. *C*, branch bearing a procarp which consists of a carpogonium (carpogonial cell) and adjacent cells. *D*, branch bearing antheridia. *E*, branch showing the cystocarps whose formation from the procarps is initiated by fertilization. To the right is a single carpospore. These are produced in the cystocarps.

ference in the number of chromosomes in their nuclei. The nuclei of the gamete-bearing plants have only half as many chromosomes as

do those of the tetrasporic plants. This is spoken of as the **haploid** number, and the number of chromosomes in the asexual plants is spoken of as the **diploid** number. The gametes have the haploid number, but as the result of the fusion of the nuclei of the two gametes the zygote has the diploid number of chromosomes and so do the carpospores and the tetrasporic plants which develop from them. One of the two nuclear divisions which occurs when the tetraspores are formed is a reduction division, and accordingly the tetraspores have the haploid number of chromosomes, as do the nuclei of the sexual plants which are produced when the tetraspores germinate. The life cycle of these plants is shown in somewhat greater detail by the following diagram, in which is also indicated the chromosome number of the various stages in the life cycle.



In each cycle the chromosome number is doubled when the gametes fuse and halved again at the reduction division just before tetraspore formation.

This alternate doubling and halving of the chromosome number is not, however, the characteristic thing about the life cycle of the red algae, for it is clear that it must take place in the life cycle of even the simplest algae having sexual reproduction, since the zygote nucleus contains the chromosomes from the two gamete nuclei. The remarkable thing about the life cycle of such plants as *Polysiphonia* is that, instead of the chromosome number being halved almost immediately as in *Oedogonium* (when the oospore germinates to form four zoospores) and in *Spirogyra* (at the germination of the zygospore), the reduction division is delayed until after the zygote has given rise to a plant body of considerable size.

A similar alternation of asexual and sexual generations occurs in all the Bryophyta, Pteridophyta, and Spermatophyta.

SUMMARY

Principal Features in the Evolution of the Algae. The Plant Body.—The simpler algae are unicellular plants, the separate cells which constitute the plant body being capable of carrying on all the necessary processes and, existing solitary or in groups without any constant form. Such plants occur in several of the classes and orders of the algae. Examples are *Synechococcus* and *Gloeocapsa* among the Cyanophyceae, and among the green algae: *Protococcus* and *Chlamydomonas*, most of the desmids, many diatoms, and others.

A somewhat more advanced condition seems to be represented by those plants in which the cells, each of which is still capable of carrying on all the essential life processes, are united into groups of a definite and constant form. Such groups of unicellular plants are called colonies. The colonies may be spherical, filamentous, in the form of flat plates, or of various other shapes. Examples of such colonies of unicellular algae are *Oscillatoria* and *Merismopedia* among the Cyanophyceae, *Scenedesmus*, *Pediastrum*, *Pandorina* and *Spirogyra* among the Chlorophyceae.

A further step in the evolution of the plant body is that by which certain cells of a relatively simple group are specialized to perform some function for the whole group (or parts of the plant body). In such plants there is actual physiological division of labor between the different parts. They are truly multicellular organisms. *Oedogonium* is a good example of such a plant. Among the cells in this plant that are specialized to perform a function for the whole are the holdfast cells, the cells which are capable of dividing, and the antheridia, oogonia, and in some species the androsporangia.

The highest step in the evolution of the plant body in the algae is illustrated by such plants as *Fucus* and the kelps. Not only are these much larger than the forms previously mentioned but they have much greater specialization of parts and tissues.

Origin and Evolution of Sex.—In the most primitive algae, reproduction is by fission. When the cells of such plants are united in colonies, the colonies may break up into groups of a few cells, each group growing by the fission of its different cells until larger colonies are formed (hormogonia production in *Oscillatoria*). Such plants may produce resistant spores (thick-walled cells with much reserve food) which can carry the organism over periods of drought or unfavorable temperature.

In several groups of algae, zoospores (motile, asexual spores) were probably produced before sexual reproduction originated. The zoospores serve for multiplication and for wider distribution of the species.

These zoospores appear to have been the structures from which gametes originated in the evolution of sex in plants. In the more primitive of plants having sexual reproduction, the gametes are alike in structure (isogametes). In less primitive forms they are structurally of two kinds (heterogametes, i.e., sperms and eggs).

In some of the forms which produce both zoospores and gametes, as in *Oedogonium*, the gametes, or at least the male gametes, are essentially the same in structure as the zoospores, though smaller in size.

In several distinct algal groups, there are slight differences in the size of the gametes of a given species, or in the duration or degree of their motility. Such species exhibit the beginnings of differentiation of the sex cells into male and female gametes.

In forms in which the gametes are further differentiated there may exist great differences in the size of the two kinds, complete loss of motility of the female gamete, and great increase in the number of male gametes produced by a single plant, together with corresponding decrease in the number of female gametes. In some of the algae in which there is a very marked differentiation of the gametes, the female gamete is retained within the gametangium (oogonium) until after fertilization.

The differences between the two kinds of gametes in heterogamous plants appear to be related to the desirability (1) of having a large amount of protoplasm and reserve food in the zygote (2) and of reducing the amount of food lost (*a*) through failure of gametes to fuse and (*b*) through the intense respiration of large, motile gametes. The following is a statement of the apparent advantages to the plant of the differentiation of gametes:

(1) A large supply of protoplasm and food for the new plant might be provided in the zygote if both of the fusing sex cells were large. This would have the disadvantage, however, that a large part of the food in the gametes would be used up in the respiration necessary to provide the energy for the movements of the gametes, for the amount of energy necessary for locomotion increases rapidly with increase in size of the body moved. In heterogamous plants there is a tendency to leave to the egg cells the rôle of providing most of the protoplasm and stored food, and to the sperm the rôle of " finding " the other gamete in order that fertilization may take place.

(2) If many large egg cells remain unfertilized there is considerable waste of material. The fact that the male gametes of many heterogamous plants are small and capable of very rapid motion without the expenditure of much energy, and the fact that they are produced in much larger numbers than are the egg cells, reduces the chance of egg cells failing of fertilization. Since only one sperm is necessary for the for-

mation of a zygote, the disproportion in numbers between the two kinds of gametes results in the failure of many sperms to function. The waste of many of these represents less loss than the waste of a single egg cell, in those species where the egg cells are much larger than the male gametes.

It must be borne in mind, however, that even among those plants in which there is very great differentiation of the gametes, there is often a very great waste of living material involved in reproduction.

Conditions Favoring Zoospore and Gamete Production.—In general, zoospores are not produced except during periods favorable to the vegetative activity of the plant. Sexual reproduction seems frequently to be brought on by conditions not favorable to vegetative activity. The zygote in many algae is a thick-walled, resistant spore, capable of withstanding conditions which would be fatal to the vegetative cells. Upon the return of favorable conditions it germinates and produces a new plant.

Relative Complexity of Algae and Typical Land Plants.—Such complexity as is characteristic of typical land plants is not found in the algae, not even in the great kelps. The relatively small number of organs and slight differentiation of tissues in the algae are sufficient for successful existence in the comparatively uniform environment of the water habitat. The plants, being largely supported in the water by their buoyancy, have less need for mechanical tissues than plants which grow erect in the air. Special tissues for absorption and conduction are less needed than in the case of land plants, since the immersed algae are entirely bathed in water, which supplies the necessary mineral salts, carbon dioxide for photosynthesis, and oxygen for respiration. Tissues for the regulation of water loss are obviously entirely unnecessary.

Alternation of Haploid and Diploid Phases in the Life History of Algae.—In these plants having sexual reproduction, the number of chromosomes in the zygote nucleus is twice the number in the nuclei of the gametes. Somewhere in the life cycle of such a plant, the "$2x$" or diploid number of chromosomes, resulting from the fusion of the two gametes, each with "x" chromosomes, must be reduced to the "x" or haploid number. In the case of the simpler algae which reproduce sexually, the reduction probably takes place at the time of the germination of the zygote (in *Oedogonium* at one of the two divisions by which four zoospores are formed from the oospore).

In certain higher algae the reduction division is delayed for a long time; in *Polysiphonia* (a red alga), for instance, it occurs during one of the two divisions of certain cells of the asexual plant by which each

group of four tetraspores is produced. (Each of these groups of four spores comes from a single cell of the asexual plant.)

In *Polysiphonia* and many other red algae, there are therefore two kinds of plants, differing as regards the number of chromosomes in their nuclei: (1) diploid plants whose nuclei have "$2x$" chromosomes and which produce asexual spores (tetraspores) having "x" chromosomes, and (2) haploid plants produced by the germination of these spores and

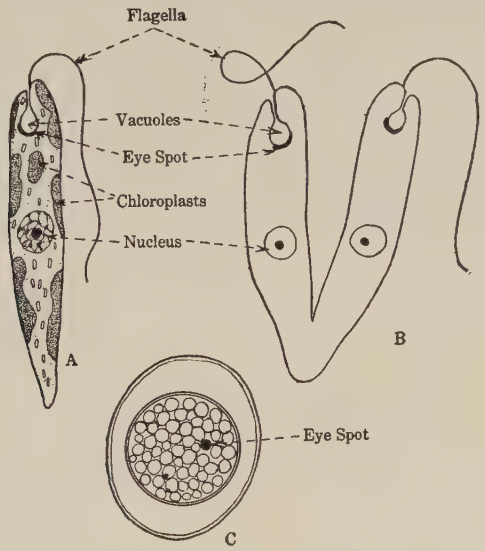


FIG. 265.—An autophytic *Euglena*. *A*, the organism in its ordinary vegetative condition. *B*, asexual reproduction by longitudinal splitting (this is a feature characteristic of the Flagellates and of certain primitive animals). *C*, a resting spore. After a time if conditions are favorable the protoplast of the resting spore divides into a number (generally four) protoplasts which are liberated from the spore and developed into individuals like that shown at *A*. The formation and germination of resting spores is a plant-like characteristic.

having "x" chromosomes in their nuclei. These plants give rise to the gametes. This production of two kinds of plants alternating with each other in the life cycle is characteristic of all the plants above the Thallophytes.

Probable Origin and Relationship of the Algae.—We have previously emphasized the fact that the algae represent not a single line of development but instead a number of lines having a common origin and showing many parallel series in their evolution. There is much

evidence to indicate that the plants in which these different lines of development had their beginning were similar to the group of living organisms called the Flagellates. The Flagellates include organisms of which some are plant-like, others animal-like, and still others combine animal and plant characteristics. They are unicellular and aquatic ciliated organisms, without definite cell wall but bounded by a dense protoplasmic layer. Some have green, yellow, or brown plastids and can carry on photosynthesis, while others are heterophytic. Many are capable, at least during part of their life cycle, of creeping amoeboid movements. Sexual reproduction does not take place among these organisms. Not only various groups of algae, and perhaps of fungi also, but in addition the simple animals called the Protozoa seem to have had their origin in the Flagellates. In Fig. 265 are shown the structure and the principal stages in the life history of one of the commonest Flagellates, *Euglena*.

CHAPTER XII

THALLOPHYTES—FUNGI

INTRODUCTION

The fungi do not constitute a natural group. Among them are included plants which are certainly more distantly related to each other than they are to certain plants outside the fungi. The single definite basis of distinction between the algae and the fungi is the fact that the algae can make their own food from simple inorganic food material, whereas the fungi, lacking chlorophyll, must secure their food ready made from some other living organisms or from the dead remains or products of some organism.

An organism deriving its food from the *living* body of either a plant or an animal is termed a **parasite.** An organism obtaining its food from the *dead* body or the non-living products of another plant or animal is called a **saprophyte.** Plant pathologists are primarily concerned with **parasitic fungi,** for these are the organisms that attack many useful living plants, derive nourishment from them and induce injuries which we call plant diseases. Plant diseases, which result from the attacks of parasitic organisms, cause tremendous losses.

There is not always a sharp distinction between parasites and saprophytes, and it is quite difficult in some cases to tell to which of these classes a given plant should be assigned. There are some fungi, for example, which may attain their best development as parasites, but which may be able for a time to exist as saprophytes. Such organisms are called **facultative saprophytes.** Also there are some fungi which normally are saprophytes in their habits, but which may now and then become parasitic, and therefore are called **facultative parasites.** These two groups are in contrast to those which are obliged to live strictly as saprophytes or parasites, as the case may be, and which are called **obligate saprophytes** or **obligate parasites.**

In the condition called parasitism, one organism, the **parasite,** secures its food entirely or in part from the tissue of another organism. The organism at the expense of which the parasite lives is called the **host.** The parasite contributes nothing to the advantage of the host.

We shall include in our discussion of the fungi an account of two groups of Thallophytes which are by many authors excluded from the fungi proper, but which are unable to make their own food. These are the first two of the classes listed in the next paragraph.

We shall consider the fungi as consisting of the following five groups:

Class 1. The Schizomycetes or Bacteria (Fission Fungi).
Class 2. The Myxomycetes (Slime Fungi).
Class 3. The Phycomycetes (Algal Fungi).
Class 4. The Ascomycetes (Ascus Fungi).
Class 5. The Basidiomycetes (Basidium Fungi).

These five classes include all the parasitic or saprophytic plants except a relatively small number which show by their structure and development that their closest relatives belong to one of the great groups of autophytic plants.

BACTERIA

General Characteristics.—The bacteria are strictly unicellular organisms. Sometimes the individuals remain more or less united and thus form irregular masses or filaments, but in such cases each cell is self-sufficient and there is no evidence of division of labor among such cells. Bacterial cells, like the cells of the Cyanophyceae, are without definite nuclei. Multiplication is entirely by fission, although the whole protoplast in some bacteria may become surrounded by a thick wall and thus form a resistant spore. The bacteria are either parasitic or saprophytic, with the exception of a very few forms which can make their own food.

Distribution of Bacteria.—These tiny organisms are all about us. They are found floating in the atmosphere, mostly as "passengers" on dust particles, up to a height of several thousand feet, except just after heavy rains or snow storms when the air is practically free of them. They are present in rain water and in freshly fallen snow, as well as in all natural bodies of water and in all drinking water which has not been boiled. They are abundant upon the surface of the human body and are present in large numbers in the intestinal tract and on all the mucous membranes. Bacteria are found in soil down to a depth of six feet and more, many millions often being present in a gram of soil. They are, of course, particularly abundant in sewage. It has been shown that there may be as many as six billion in a cubic inch of sewage. Living bacteria are present on the surface of all the objects about us except those which have recently been heated to a high temperature or otherwise sterilized. They are seldom found within the

tissues of plants and animals except when the organisms are suffering from one of the numerous diseases which bacteria may cause.

Size of Bacteria.—These organisms are very small but they vary in size within rather wide limits. Among the smallest known bacteria is a rod-shaped form which is $\frac{1}{2}$ micron long and $\frac{1}{5}$ micron wide, but the average dimensions of the rod-shaped forms are probably about 2 microns by $\frac{1}{2}$ micron. (A micron, the unit of microscopic measurement, is $\frac{1}{1000}$ of a millimeter or about $\frac{1}{25000}$ of an inch.)

Multiplication of Bacteria.—A bacterium which is abundantly supplied with food and surrounded by conditions favorable to it will grow to a certain maximum size and then divide by fission into two bacteria of equal size. Under favorable conditions the organisms increase in number by this method very rapidly, so that the descendants of a single bacterium may be, within a few hours, literally countless. Some bacteria may divide as often as once in twenty minutes. It has been estimated that if the cholera organism maintained its maximum rate of fission for twenty-four hours, the bacteria which would thus be produced from one bacterium would number 1,600,000,000,000,000 and would weigh almost half a million pounds. This number is, of course, quite beyond our conception, but we gain some idea of its immensity when we learn that it is about twenty-five thousand times the number of seconds since the birth of Christ. If the same rate of division were maintained for two days, the number of individuals resulting would be 2 to the 96th power, a number with 28 ciphers. That number of organisms would weigh about a trillion tons. As a matter of fact, long before any such number of bacteria could be produced by fission, the processes of growth and division would have been slowed down or entirely interrupted by the exhaustion of the food supply or by the accumulation of poisonous waste products of metabolism (chemical changes in the living organism).

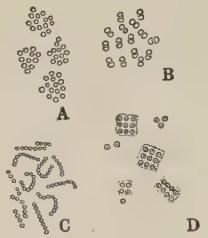


Fig. 266.—Coccus forms of bacteria. *A*, *Staphylococcus*. *B*, *Diplococcus*. *C*, *Streptococcus*. *D*, *Sarcina*. All magnified about 1000×.

Form Types of Bacteria.—There are three principal morphological types of bacteria: spheres, rods and spirals. These are spoken of respectively as **cocci** (singular coccus), **bacilli** (singular bacillus), and **spirilla** (singular spirillum).

Structure of the Bacterial Cell.—Many bacteria have the cell wall surrounded by a capsule or envelope of gelatinous material. In some forms this gelatinous mantle holds the bacteria together after division,

so that they form filaments or irregular masses. This is the case with the bacteria which are responsible for the production of vinegar. The gelatinous mass with embedded bacteria is the so-called "mother of vinegar." The cell wall proper differs from that of typical plants in that it contains no cellulose. It is very similar chemically to the protoplasm itself. The protoplast consists of cytoplasm, through which are scattered particles of chromatin. That the protoplast is bounded by a semi-permeable membrane is clear from the fact that the bacterial cell may be plasmolyzed. This fact is the basis of the commonly used methods of preserving food from spoiling by bacteria and similar plants through the use of salt and sugar. When foods are preserved in sugar, sugar syrup, dry salt, or brine, the bacteria are unable to grow because of the withdrawal of most of their water by osmosis.

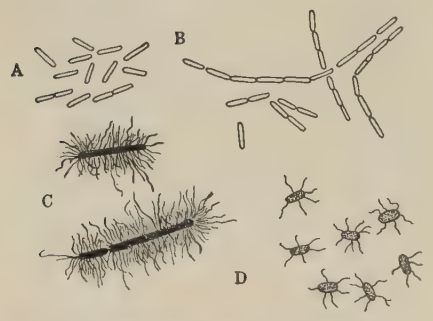


FIG. 267.—Bacillus forms of bacteria. *A*, *Bacillus sporogenes*. *B*, *Bacillus subtilis*. *C*, *Bacillus proteus*. *D*, *Bacillus typhosus*. All magnified about 750×.

Spore Formation.— Some bacteria are capable of producing resistant spores. These structures can withstand high temperatures, the presence of poisonous substances, and other unfavorable conditions which are fatal to the ordinary vegetative cell. Fortunately, only a few disease-producing bacteria form spores. With few exceptions, the spores are produced singly within the vegetative cells. The protoplast contracts, probably as the result of loss of water, and becomes surrounded by a relatively thick wall. Generally, the wall of the cell within which the spore is formed is later dissolved away and thus the spore is freed.

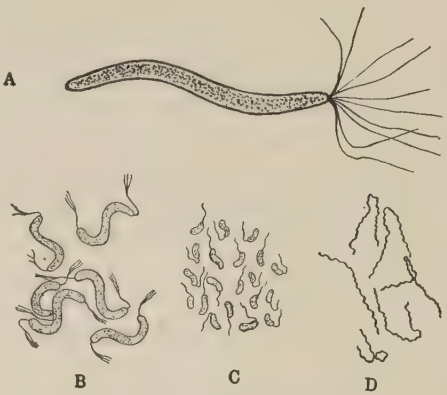


FIG. 268.—Spirillum forms of bacteria. *A*, a species of *Thiospirillum* (a sulphur oxidizing organism). *B*, *Spirillum undulum*. *C*. *Vibrio cholerae*. *D*, a species of *Spirochaete*. All magnified about 1000×.

Koch, a great pioneer student of bacteria, found that the spores of *Bacillus anthracis*, which is the organism causing anthrax, could remain alive as long as fifteen days in a 1 per cent carbolic acid solution, whereas the ordinary vegetative cells of the same organism were dead after two minutes in such a solution. Spores are also much more resistant to heat than are vegetative cells. Those of *Bacillus subtilis*, a bacterium always abundant on hay, survive one-half to three-quarters of an hour of boiling, while the vegetative cells are killed at once by boiling water. The spores of some bacteria are known to be more easily killed by light than are the vegetative cells.

Germination of Spores.—When temperature, moisture, food supply, and other conditions are favorable, bacterial spores germinate and each gives rise to a single bacterium. Apparently the spore wall first undergoes a softening and then the contents swell as a result of water absorption. The spore wall is then broken through at one point, the protoplasm pushes out, surrounds itself by a new cell wall, and thus a new bacterium is formed. Since but one spore is produced within a vegetative cell and since each spore gives rise upon germination to a single bacterium, it is evident that spore formation is not a method of multiplication. The spores serve rather to tide the plant over a period which is unfavorable to vegetative activities.

Motility of Bacteria.—Some bacteria are able to swim about in a liquid medium. This active locomotion is accomplished by means of long and slender threads, or whips of protoplasm, called **cilia** (singular **cilium**) or **flagella** (singular **flagellum**). These may arise from various parts of the cell. By their rapid spiral motion they cause the bacterium to move about through the water or other liquid medium. Cilia have never been observed among the *Trichobacteria;* they are very rare among the cocci, not infrequent among bacilli, and practically universal among the spirilla.

Beneficial Activities of Bacteria.—These plants are popularly looked upon as organisms which are always harmful to man or to man's interests. This is but natural in view of the prominence which has been given to them as the causative agents in human and animal disease. Great as is the loss of life and property and the suffering for which some bacteria are responsible, the beneficial effects of bacteria doubtless outweigh the harm which they do.

Their greatest single service is no doubt the part they play, together with the yeasts and molds, in causing the decay of plant and animal bodies. Through this process the carbon, oxygen, hydrogen, nitrogen, sulphur, and phosphorus which make up the bodies of animals and plants and their products are reduced to simple compounds, such as

carbon dioxide, water, nitrates, sulphates, and phosphates, which can again be used as raw material in food building by living plants. Were it not for this process of decay, in which bacteria play so important a part, much of the available supply of certain essential elements would remain permanently locked up in the dead bodies of organisms, so that what remained would not be sufficient for the growth and development of living plants and animals.

The fertility of agricultural soils is largely dependent upon the presence of certain bacteria, which not only make available certain of the essential elements already in the soil, but may increase the fertility of the soil by adding to the amount of nitrogen present in it. Bacteria are also essential to various industrial processes of great importance. In several stages through which leather must pass in the process of tanning, bacterial action is involved. The formation of vinegar is impossible without bacterial activity. The preparation of the flax fiber, used in the manufacture of linen cloth, includes a stage, called "retting," during which the flax stalks are submerged in water and subjected to the action of bacteria which digest the pectose between the bast fibers and free these from each other. The ripening of cream by certain bacteria is the source of the characteristic flavors of the best butter, and some of the most prized cheeses owe their fine flavor at least in part to bacterial products. The curing of tea and the manufacture of indigo are other examples of processes in which bacterial action is involved, and the same is true of the preservation of corn and other fodders in the form of ensilage, and of cabbage as sauerkraut.

Harmful Activities of Bacteria.—Bacteria are the causative agents in a large number of human diseases, including diphtheria, tuberculosis of the lungs and other organs, anthrax, meningitis, typhoid fever, cholera, pneumonia, lockjaw, leprosy, and many others. Most of the serious diseases of domestic animals are also bacterial. Some of the most important are glanders, tuberculosis of cattle, hogs, and fowls, blackleg, anthrax, and chicken cholera. Whereas relatively few of the diseases of man and of animals are caused by any fungi except the bacteria, most of the diseases of plants are caused by higher fungi and relatively few by bacteria. Among the few bacterial diseases of economic plants are fire blight of pears, wilt of egg plant, potato, cucumber, squash, and watermelon, walnut blight, and the soft rots of various vegetables.

Bacteria are also a source of serious loss to man because of the spoiling of food which is caused by them and by certain other fungi. It is this fact which makes necessary the expensive measures which we take for preserving surplus meat and other food by means of drying,

salting, pickling, canning, and preserving in sugar. In addition to the soil bacteria which increase the fertility of agricultural soils, there are some which injure the soil by causing the loss of part of its combined nitrogen.

Fermentation.—Under the general term, **fermentation,** we shall include all those chemical changes involved in the breaking down by bacteria and by other fungi, of the proteins, carbohydrates, and fats of the bodies of plants and animals or of their products. The organisms accomplish their characteristic chemical changes by the action of enzymes which they produce.

Protein Fermentation.—Different groups of bacteria are responsible for the fermentation of each of the three classes of food substances, and no doubt often for different substances in each class. The term **decay** is generally applied to the fermentation of proteins when it takes place in the presence of oxygen and when it is therefore not attended by offensive odors. When protein fermentation goes on under anaerobic conditions (in the absence of an abundant supply of oxygen), substances of offensive odor are produced and the process is spoken of as **putrefaction.** In these processes the very large and complex protein molecules are broken down, mostly by a process of hydrolysis (union of a complex compound with water and its subsequent splitting into two simpler substances), into the following and other successively simpler compounds: **proteoses, peptones, polypeptids, peptids,** and **amino-acids.** The amino-acids may then finally be broken down, probably by bacterial species that are not concerned in any of the earlier steps of protein fermentation, into such very simple substances as ammonia, gaseous nitrogen, hydrogen gas, carbon dioxide, hydrogen sulphide, methane (marsh gas), and water. The bacteria concerned secure food for their own bodies from the substances fermented, and, from the decomposition of these substances, the energy which they need for their own life process. It has been shown in many cases that enzymes produced by the bacteria are the direct cause of the decomposition concerned, and these enzymes, even when separated from the protoplasm of the bacteria, are able to bring about the characteristic changes.

Fermentation of Fats.—Probably a large number of different kinds of bacteria may bring about protein fermentation, but there seem to be relatively few forms which are capable of fermenting fats. However, a considerable number of other fungi may carry on this process. The fermentation of fats is largely a process of hydrolysis. A molecule of fat is united with a water molecule and then split into a molecule of glycerine and a molecule of a fatty acid. Both of these can be still further broken down by other organisms.

Fermentation of Carbohydrates.—The processes of carbohydrate fermentation are of great economic importance, one of the most important being **alcoholic fermentation.** Only a few bacteria are able to carry on this process, the most important agents being the yeasts, a group of unicellular fungi which are commonly considered to be primitive Ascomycetes. They transform glucose and other similar sugars (hexoses) into ethyl alcohol and carbon dioxide, according to the following equation:

$$\underset{\text{(glucose)}}{C_6H_{12}O_6} = \underset{\text{(ethyl alcohol)}}{2C_2H_5OH} + \underset{\text{(carbon dioxide)}}{2CO_2}$$

This is an energy-yielding reaction and the yeast actually respires the sugar, using part of the energy thus secured for its own life processes. The fermentation of sugar by yeast is an enzyme reaction, although for many years all attempts to separate a sugar-fermenting enzyme from yeast failed. It was finally shown that **zymase,** the enzyme involved, is an intracellular enzyme. That is to say, it can not escape under natural conditions from the cell within which it is produced. The substances acted upon by such an enzyme must pass by diffusion into the living cell before they can be changed. The products of the enzyme's action may then pass out of the cell by diffusion. The liquid in which yeast cells are growing does not contain zymase in solution and therefore does not cause fermentation of sugar when freed of yeast cells. Zymase was finally secured by freezing the yeast cells, grinding them into a fine powder, and then treating them with water. When the water was filtered free from the fragments of yeast cells, it was found capable of causing fermentation. Cane sugar ($C_{12}H_{22}O_{11}$) can not be fermentated by the enzyme zymase, but many yeasts produce another enzyme, called **sucrase,** which brings about the hydrolysis of cane sugar with the formation of the two hexoses, fructose and glucose. The fermentation of hexose sugars is really an incomplete respiration carried on by the yeast cells. If there is an abundant supply of oxygen they can carry on ordinary and complete respiration of this sugar with the production of carbon dioxide and water.

Starch is a carbohydrate which yeasts are generally unable to ferment. In the brewing industry the starch of barley and other grains must be changed to sugar by the process of malting before fermentation can take place. In malting, the grain is allowed to germinate and the **diastase** produced by the seed during germination changes the starch of the seed into sugar.

Yeast is used in baking because the carbon dioxide liberated by the fermentation of a small part of the sugar contained in the dough forms bubbles and thus renders the bread "light."

Acetic Acid Fermentation.—After alcoholic fermentation has progressed to a certain point, the concentration of alcohol becomes so great as to kill off the yeast organisms or at least prevent their further activity. Then, if the solution contains not more than about 14 per cent of alcohol and if it is exposed to the air, acetic acid bacteria, which were already present or which have entered from the air, increase rapidly in number and bring about acetic acid fermentation. In this process alcohol is converted into acetic acid and water. This change is an oxidation and will therefore not go on unless considerable quantities of oxygen are available. The following equation represents this change:

$$\underset{\text{(alcohol)}}{C_2H_5OH} + \underset{\text{(oxygen)}}{O_2} = \underset{\text{(acetic acid)}}{CH_3COOH} + \underset{\text{(water)}}{H_2O}$$

The enzyme that brings about this change has not been isolated but it is probably an intracellular one. After practically all the alcohol has been converted into acetic acid and water, the acid may be decomposed with the formation of carbon dioixde and water. The bacteria of acetic acid fermentation utilize the alcohol as a source of food and secure from its fermentation (an exothermic process) energy for their own use.

Lactic Acid Fermentation.—Another carbohydrate fermentation, and one carried on principally by bacteria, is lactic acid fermentation, in which milk sugar (lactose) is changed into lactic acid. It is the production of this acid which causes the souring of milk, and the coagulation of the protein (casein) which is ordinarily called curdling. When the acid has reached a certain concentration, which differs according to the type of lactic acid bacteria which are principally involved, the fermentative activity of the bacteria ceases. Although the lactic acid bacteria are a source of serious loss because of the quantities of milk which they make useless for ordinary consumption and because of the effort and expense which are necessary to prevent the souring of milk before use, their activities are not entirely harmful. The lactic acid bacteria are useful to the producer of butter because the presence of lactic acid in the cream increases the yield of butter and improves the flavor as well. They are also necessary to the production of sour-milk cheeses. The curd used for sweet-milk cheeses, however, is produced by the coagulating enzyme, rennet, which is introduced by the cheesemaker.

Bacteria in Relation to Soil Fertility.—Of the essential materials for food manufacture secured by the green plant from the soil, nitrogen is, next to hydrogen and oxygen, the one which is needed in largest

quantities. This element makes up a large part of the molecule of the different proteins of which protoplasm largely consists. Because it is needed in such quantities by the plant, soil nitrogen is the element most likely to become insufficient in quantity, after repeated cropping of the soil, than any of the other essential elements. Large quantities of the nitrogen from the soil which has been built into plant proteins is removed in the form of stored food in the grain or other useful parts. Although the waste products from domestic animals, containing much of the nitrogen of the food which they have eaten and utilized in their metabolism, is in part returned to the soil as fertilizer, much of the nitrogen of the crops removed from the soil is never returned to it, but is altogether wasted or even discharged into and allowed to pollute our rivers. As a result, maintenance of the supply of soil nitrogen is one of the principal problems of soil fertility.

Nitrogen Fixation.—The atmosphere contains about 80 per cent of gaseous nitrogen. It has recently been reported that certain cereals are able to secure a very small part of their nitrogen from the gaseous or free nitrogen of the air, but it is certainly true that they must secure most of their nitrogen in some other form. In the absence of all nitrogen except free nitrogen, the higher plants do not thrive. Nitrogen in the form of nitrates (salts in which nitrogen and oxygen, in the proportion of one atom to three, are united with some metal, as in $NaNO_3$, KNO_3 and $Ca(NO_3)_2$), is the most favorable for the use of crop plants. Nitrogen in the form of ammonium salts (salts in which nitrogen and hydrogen, in the proportion of one atom to four, as $(NH_4)_2CO_3$ and NH_4NO_3), can also be used but is less favorable. A number of agencies can cause the free or gaseous nitrogen of the atmosphere to unite with other elements and thus make it available for the use of green plants. The union of free (gaseous) nitrogen with some other element or elements to form a compound is called **nitrogen fixation.** The common methods by which nitrogen fixation takes place in nature are (1) electrical discharges in the atmosphere, (2) activity of bacteria living free in the soil, and (3) activity of bacteria living symbiotically.

Electrical discharges in the atmosphere, both in the form of lightning and in the form of silent discharges, which are constantly taking place between the atmosphere and the earth, bring about the union of small quantities of atmospheric nitrogen and oxygen. The resulting oxides of nitrogen are washed from the air by rain and thus reach the soil, where they combine with other substances to form nitrates. The quantity of fixed nitrogen which thus reaches the soil, is, however, exceedingly small.

Nitrogen Fixation by Bacteria Living Free in the Soil.—It can be

shown that bare soil, even when it is prevented from receiving any nitrogen compound from the atmosphere, may increase in the amount of combined nitrogen which it contains. It is not difficult to demonstrate that this is due to bacteria present in the soil, for in sterilized soil no such increase in combined nitrogen takes place. These nonsymbiotic nitrogen-fixing bacteria have the power of combining the nitrogen of the air in the soil with other elements and thus building up complex organic nitrogen compounds. These complex compounds are later broken down in the soil and form nitrates. The best known nitrogen-fixing bacteria living free in the soil are *Clostridium pasteurianum* and several species of *Azotobacter*. This bringing of the free nitrogen into combination with other elements is an energy-absorbing process, and the necessary energy for it is secured by the bacteria from the oxidation (respiration) of organic carbon compounds in the soil.

Nitrogen Fixation by Symbiotic Bacteria.—In addition to the nitrogen-fixing bacteria which live free in the soil, there are others which live in the roots of certain flowering plants, particularly members of the Leguminosae (bean family). The nitrogen-fixing bacterium which is commonly found in the roots of various beans, peas, lupines, clovers, and other leguminous plants, is called *Pseudomonas radicicola*. There are various strains of this organism, each of which seems to prefer association with certain species of leguminous plants. The bacteria gain entrance to the roots when the latter are young, and by their presence cause the formation of swellings or tubercles upon the root. The cells of these tubercles are largely filled with the bacteria. The atmospheric nitrogen is probably fixed by these organisms in the form of organic nitrogen compounds. The seed plant bearing the tubercles is able to absorb and to use this organic nitrogen, or some simpler nitrogen compound arising from its partial decomposition. The relation between *Pseudomonas radicicola* and the leguminous plant is certainly one of **symbiosis** (living together of two kinds of organisms with mutual benefit). The bacteria secure food from the protoplasm of the leguminous plants in whose roots they live, and the legume secures nitrogen from the bacteria. Seedlings of leguminous plants, grown in sterilized sand and provided with all the essential substances except combined nitrogen, develop no tubercles and soon show evidence of nitrogen shortage. If plants grown under such conditions and showing evidence of lack of nitrogen are watered with a soil extract from unsterilized soil in which legumes have grown, *Pseudomonas radicicola* is introduced, tubercles are formed, and the plants thrive. Even though the plants are cut and removed from the field, there is an increase in the amount of combined nitrogen in the soil in which a legume crop has grown.

The roots left in the soil and the tubercles which they bear undergo decay, and the combined nitrogen within them finds its way into the soil. There it is converted into nitrates. A number of plants, among others the common alder (*Alnus*), usually have nitrogen-fixing bacteria growing in symbiosis with them, and stimulating the roots to tubercle formation.

Nitrification.—Considerable ammonia is liberated into the soil as a result of the decay there of proteins from dead organisms or their organic products. If this remained in the form of ammonia gas it would diffuse into the atmosphere and thus be lost to the soil in which it was produced. Actually most of it is combined in the soil with other substances to form salts, such, for instance, as ammonium carbonate, $(NH_4)_2CO_3$. It has been observed that, even in bare soils, the quantity of nitrogen in the form of ammonium compounds tends to decrease, and that the quantity of nitrogen in the form of nitrates tends to increase proportionally. This conversion of ammonium nitrogen into nitrate nitrogen was formerly believed to be a simple chemical change with which organisms had nothing to do. It has been shown, however, that this change of ammonium salts into nitrates does not take place if the soil has been sterilized, an indication that organisms of some sort are concerned in the process. This transformation is known to take place in two stages: (1) the conversion of ammonium nitrogen into the nitrogen of nitrites, such as KNO_2 and $Ca(NO_2)_2$; and (2) the conversion of nitrites into nitrates. The two stages are carried on by different bacteria. The first step is performed by several species of the genus *Nitrosomonas*, and the second by bacteria belonging to the genus *Nitrobacter*. These two kinds of organisms always occur together and are common in soils, manure heaps, river water, and sewage. As rapidly as nitrite is formed by *Nitrosomonas* it is converted into nitrate by *Nitrobacter*, so that in some cases it is not possible to detect nitrites in soils in which nitrification is going on. Neither of these organisms can thrive in the presence of large quantities of carbohydrates or of other easily oxidized organic compounds. Accordingly, the nitrification is not active in very heavily manured soil until other bacteria have fermented most of the organic material.

Favorable soil conditions for active nitrification are sufficient lime and good tillage and drainage. Tillage and drainage are important in order that the soil may be well aerated and that thus sufficient oxygen may be available for the oxidation of ammonium nitrogen to nitrate nitrogen.

Nitrosomonas and *Nitrobacter* are autophytic plants. They are like green plants in that they are able to manufacture their own food from

water and the carbon dioxide of the air or that easily secured from bicarbonates in the soil. They differ from green plants, however, in that they can carry on this synthesis of food in the dark. They secure the energy for this endothermic process not from light but from the

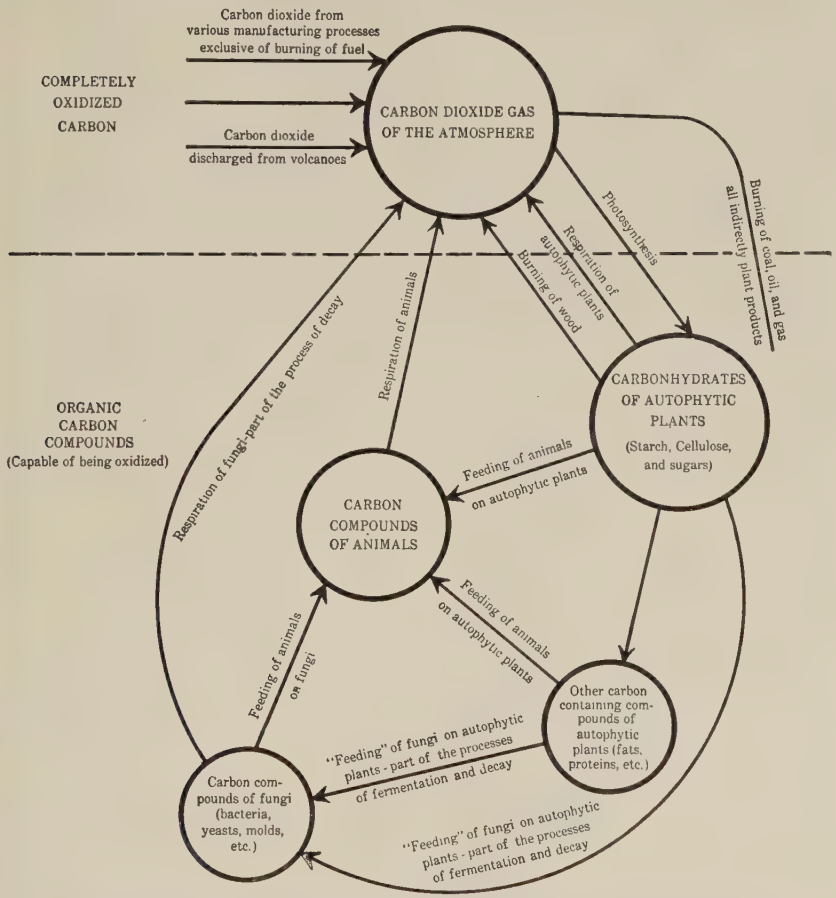


FIG. 269.—Carbon cycle diagram, showing the principal sources of the carbon dioxide of the atmosphere and the principal changes which it may undergo in organisms.

oxidation of ammonium-nitrogen to nitrite and of nitrite to nitrate, these two latter processes being themselves exothermic. Thus these organisms are as truly autophytic as green plants. Supplied with ammonia or nitrates by the oxidation of which they secure the energy necessary for food manufacture they could live in a world containing no other kind of organisms. Similarly certain other bacteria live auto-

phytically, securing their energy for food synthesis by the oxidation of hydrogen sulphide (H_2S) to sulphur and finally to sulphuric acid sulphur (H_2SO_4). There are several kinds of autophytic bacteria. Such food manufacture by use of energy secured from a chemical reaction (oxidation of ammonia, nitrite, hydrogen, sulphide, etc.) is called **chemosynthesis** in contrast with photosynthesis which utilizes the energy of light.

Denitrification.—There have been found in soil and in manures, as well as in the air and in natural bodies of water, bacteria which, instead of increasing the quantity of nitrate nitrogen, carry on the reverse process and convert nitrates into nitrites, into gaseous oxides of nitrogen, or even into free nitrogen. If this process of denitrification results in the formation of free nitrogen, the nitrogen passes into the air and is lost from the soil. Some of these harmful denitrifying bacteria are most active in soil which is poorly drained and therefore not well aerated. Large quantities of unfermented organic matter encourage the denitrification process. Accordingly, very heavy dressing of soil with unrotted manure is in general to be avoided. Unless very great quantities of organic matter are added to the soil, there is no danger of cultivated soils in which nitrification has taken place suffering from denitrification; for before nitrification could have taken place most of the organic material must have been oxidized.

The Carbon Cycle and the Nitrogen Cycle.—We have repeatedly referred to the fact that autophytic plants build up the simple inorganic substances, water, carbon dioxide, and salts containing calcium, potassium, magnesium, iron, sulphur, nitrogen and phosphorus, into relatively complex organic substances which constitute the food not only of these green plants but also of all animals and heterophytic plants. These organic substances are broken down again in the destructive processes (notably respiration) which go on in all living organisms. In the dead bodies of plants and animals and in the excretions of animals there are large quantities of carbon, nitrogen, and the other essential elements (in the form of organic compounds), which are not available for the use of green plants. If it were not for the bacteria and other fungi which bring about the fermentation of proteins, carbohydrates, and fats, these essential elements would remain permanently locked up in dead organisms and animal excretions. In time so much carbon and nitrogen would be removed from "circulation" as the result of this "hoarding" of the natural supply, that autophytic plants could no longer live and therefore all other organisms would soon succumb.

Fortunately for the continuance of life on the globe, various bactria and other fungi can "unlock" the organic compounds of dead

plants and animals and of the excretions of animals and convert the essential elements into forms in which they can be used again as raw material for food manufacture by autophytic plants. Thus it is that

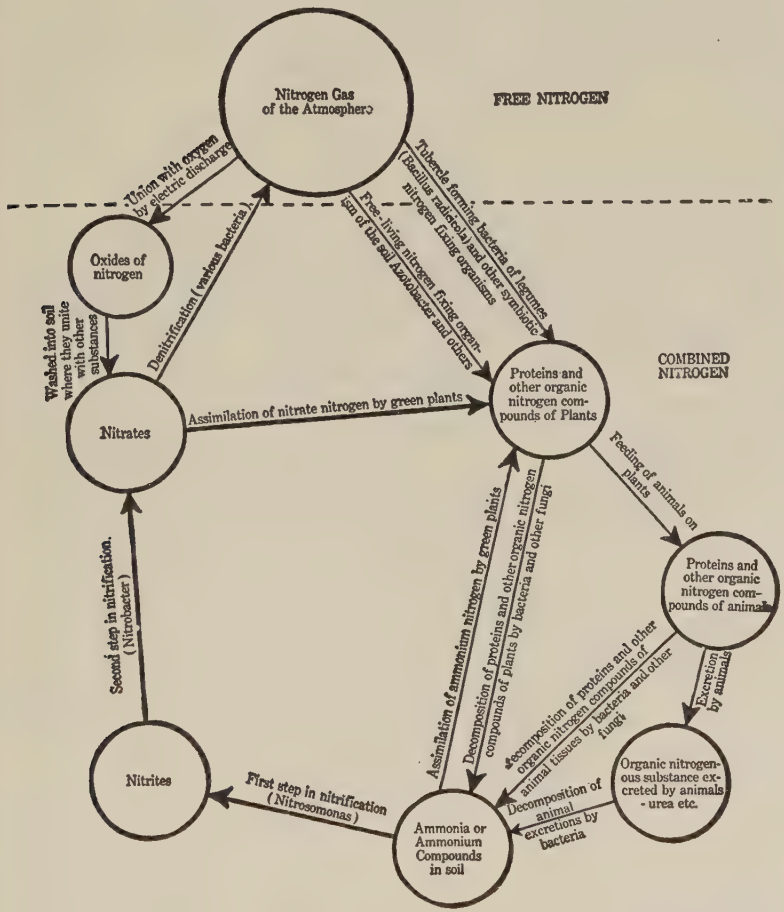


FIG. 270.—Nitrogen cycle diagram, showing the principal changes in form which nitrogen may undergo in organisms.

these elements pass repeatedly through a cycle in which they are first converted from simple to complex compounds and then returned to the simple form by respiration, or by fermentation by bacteria and other fungi. If we could trace the history of any nitrogen or carbon atom,

for instance, we might find that it had been part of hundreds of different organisms in succession; that it had literally "transmigrated" from an oak, to a bacterium, to a wheat plant, to a man, to a worm, and thus through innumerable changes throughout the ages since life first appeared upon the earth. The principal changes which carbon and nitrogen may undergo in one such cycle are graphically shown in the accompanying diagrams (Figs. 269 and 270).

MYXOMYCETES

Characteristics of the Myxomycetes.—In the Myxomycetes there seems to be a combination of animal and plant characteristics, and on this account these organisms have excited the interest of both botanists and zoologists. During the vegetative part of their existence these plants consist of multinucleate masses of naked protoplasm, and are capable of amoeboid movement (movement by flowing of living substance), and of engulfing solid food particles. These characteristics —absence of cell walls, locomotion by streaming of protoplasm, and ability to take solid food particles into the protoplasm—are generally considered to be animal characteristics. In their reproduction, however, the Myxomycetes are more like certain plants (some kinds of fungi) than they are like any animals, and their spores have cellulose walls, another plant characteristic. With the exception of two or three parasitic genera, they are all saprophytes, securing their food from the decaying leaves and twigs and rotting wood of moist habitats, mostly in the forests. Because of their delicate structure and occasionally brilliant coloring, many of the Myxomycetes are of remarkable beauty.

Life History of Typical Myxomycetes.—One of the most widespread and common genera of Myxomycetes is *Stemonitis*, which we shall use as a type of the class. In the ordinary vegetative condition the plant consists of a slimy mass of protoplasm, termed a **plasmodium** (plural, **plasmodia**). There are no walls surrounding the plasmodium and the numerous nuclei are distributed throughout the general cytoplasm without separating walls. The protoplasm exhibits a streaming motion and creeps about over the surface of its substratum by extending and withdrawing portions of its body. These arm-like processes are called **pseudopodia** (singular, **pseudopodium**). The plasmodium is sensitive to light and while in its vegetative state, avoids strong light, creeping about on the surface of logs and among decaying leaves and sticks in moist and shady places. Just before the reproductive stage begins it

moves from the shade and into drier, more elevated and more highly lighted places.

After a while locomotion ceases, and then spore-containing structures (sporangia) are developed either singly or in groups. A typical sporangium, such as occurs in *Stemonitis* and *Arcyria,* consists of an enlarged upper portion in which the spores are formed and a slender stalk which is attached to the substratum. The sporangium is covered with a hardened envelop, termed the **peridium.** The internal protoplasm of the sporangium usually differentiates into the following: (1) **spores,** each of which is uninucleate and surrounded by a cellulose wall, and (2)

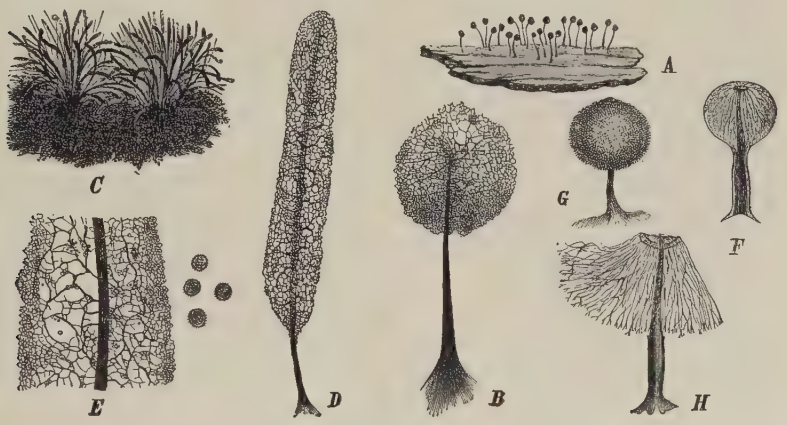


FIG. 271.—Myxomycetes. *A–B. Comatricha nigra; A,* group of sporangia, natural size; *B,* a single sporangium enlarged showing the stalk and the net-like capillitium. *C–E, Stemonitis fusca; C,* sporangia, natural size; *D,* a single sporangium enlarged showing the stalk and capillitium; *E,* portion of capillitium and spores. *F–H, Enerthema papillatum; F,* unripe sporangium; *G,* mature sporangium; *H,* capillitium. (*C, D,* after Harshberger. *A, F, G, H,* after Rostafinski; *B, E,* after de Bary; all from Harshberger's *Mycology and Plant Pathology.*)

capillitium, consisting of simple or branching tubes or threads. The spores are enmeshed in the network of the capillitium, which is hygroscopic and by its movement discharges the spores after the drying and breaking of the peridium. The spores are then dispersed by the wind. In the germination of the spore, for which abundant water is essential, the wall is ruptured and the contents escape as a naked amoeboid protoplast. Later it develops a single **flagellum** or **cilium,** by the motion of which the body is propelled about in the water. These ciliated motile protoplasts multiply rapidly by division. After a time each loses its cilium, becomes amoeboid and may multiply by fission.

FIG. 272.—A cabbage plant affected with club-root (*Plasmodiophora brassicae*). Note the hypertrophied roots, the thin stem and the absence of a head due to disease. (From Chupp, in Cornell Agricultural Experiment Station Bulletin.)

After a time these uninucleate amoeboid cells come together in groups and coalesce to form a plasmodium.

The stages in the life history of a typical myxomycete may be summarized as follows: plasmodium—sporangium—spores—amoeboid uninucleate protoplasts—ciliated stage multiplying by fission—another amoeboid stage—coalsecence—plasmodium.

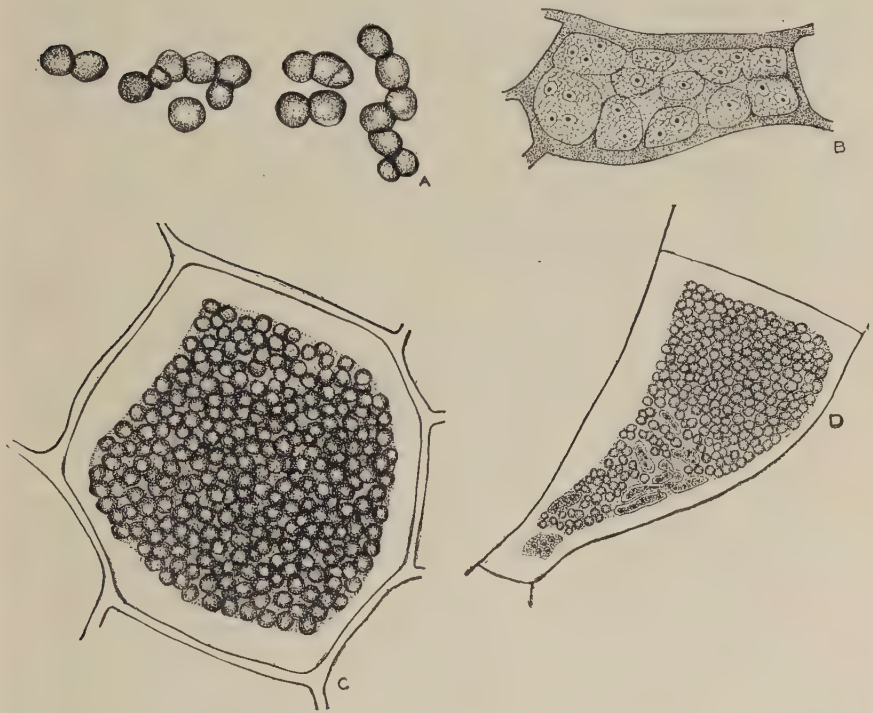


Fig. 273.—Club root of cabbage (*Plasmodiophora brassicae*). *A*, spores. *B*, a host cell filled with amoeboid cells of the parasite. *C*, cell of the host filled with spores. *D*, a cell of the host showing the formation of spores from the protoplasm of the parasite. (After Chupp, in Cornell Agricultural Experiment Station Bulletin.)

Club Root of Cabbage.—This is a destructive root disease of cabbage and other crucifers, caused by the myxomycete, *Plasmodiophora brassicae*. This parasitic slime fungus lives chiefly in the parenchyma cells near the root cambium, in which the parasite in the amoeboid form may be detected in an early stage of the disease. As a result of its presence, there is abnormal enlargement of the individual cells of the host, an increase in the number of cells, and the development of malformations. At maturity of the host the invaded cells are found

to be filled with spherical thick-walled spores. The different stages in the life history of this organism are as outlined above, in the case of *Stemonitis*, except that no true sporangia are developed.

PHYCOMYCETES

Characteristics.—This class of fungi is called the Phycomycetes (alga-like fungi) because of the close resemblance which they show to certain algae (1) in the structure of the filaments (hyphae) which make up the plant body, and (2) in their method of reproduction. The hyphae are, like the filaments of *Vaucheria*, that is, coenocytic filaments without cross walls except where the reproductive organs are cut off. The absence of cross walls in the hyphae is characteristic, and by this vegetative feature alone they can usually be distinguished from the sac-fungi (Ascomycetes), and the basidium-fungi (Basidiomycetes) both of which groups have **septate hyphae.**

Two sub-classes of Phycomycetes are recognized, the Oomycetes and the Zygomycetes. The principal orders of each are given below, together with a few representative genera.

I. **Oomycetes.**—Heterogamous; zoospores produced by most forms; generally aquatic. The principal orders are:

(*a*) *Chytridiales.*—This group includes the lowest of the Phycomycetes. Many of them are parasitic on algae and upon other fungi and a few are parasitic upon higher plants.

(*b*) *Saprolegniales.*—The members of this group are commonly called water molds. Many of these occur in ponds and streams on the dead bodies of insects, and on other organic matter. Several species attack fish, producing a serious disease. One species, *Pythium de Baryanum*, is one of several fungi which may cause the common disease of seedlings known as **damping off.** A representative group in this order is the genus *Saprolegnia*, which contains many species.

(*c*) *Peronosporales.*—This is a large group of parasitic forms which are commonly known as the **downy mildews.** The principal genera are *Albugo*, *Plasmopara*, *Peronospora*, and *Phytophthora.*

II. **Zygomycetes.**—Isogamous; no zoospores; mostly aerial forms. The principal orders are:

(*a*) *Mucorales.*—These are the black molds, and are mostly saprophytic. Common bread mold, *Rhizopus nigricans*, is the best-known representative.

(*b*) *Entomophthorales.*—The members of this group are parasitic on insects.

SAPROLEGNIA (WATER MOLD)

Most of the species of *Saprolegnia* are saprophytes. These saprophytic species are common in streams and ponds on the bodies of dead insects, and crustacea and other decaying organic matter. A few species are parasitic and attack living fish or fish eggs, being particularly destructive when they infest the eggs and young fish in the hatcheries. Water molds may easily be obtained for study by placing dead flies in stagnant water. Within a few days, the insects generally become surrounded by a whitish growth of *Saprolegnia* or some other member of the family to which it belongs.

The Plant Body.—The plant body consists of numerous branched filaments or hyphae which are coenocytic in structure. These nonseptate, multinucleate hyphae penetrate the substratum (material upon which they live) and absorb organic substances which are used as food and which make possible the growth of hyphae.

Asexual Reproduction.—After a period of vegetative activity, hyphae grow out to the surface of the substratum and protrude into the surrounding medium. Some of these filaments become swollen at the tip, and cross walls are formed, separating the swollen portions from the rest of the hyphae. This terminal structure becomes a **sporangium,** its contents dividing up into a large number of **zoospores,** each having a single nucleus and two cilia borne at one end. After escaping through a terminal pore, they swim about in the water for a time, come to rest, withdraw their cilia, and form a wall. Later, each one of these produces a single zoospore with two cilia attached laterally, which swims about in the water and, if it comes to

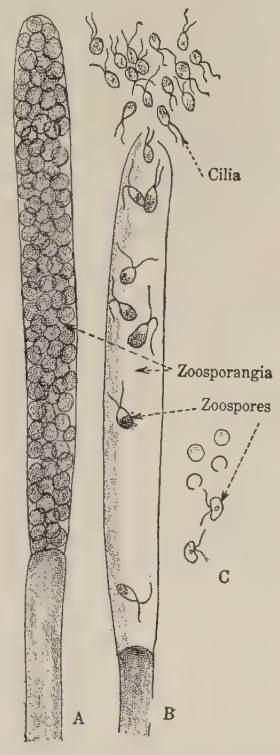


FIG. 274.—*Saprolegnia* showing asexual reproduction. *A*, a mature zoosporangium a short time before the liberation of the spores. *B*, a zoosporangium discharging zoospores which have terminal cilia. *C*, several of these zoospores which have become encysted; also two of the laterally biciliate zoospores which develop from the encysted zoospores.

rest on suitable material, sends out tubular outgrowths which penetrate and infect this new material. It is not clear what is the significance of the formation of the two different zoospore stages in the life history of *Saprolegnia*. The asexual method of reproduction in *Saprolegnia* resembles that in *Vaucheria*. In both genera, the zoosporangia develop as terminal cells. It will be recalled that in *Vaucheria* a single multinucleate and multiciliate zoospore is produced in each sporangium and that the cilia occur in pairs, with a single nucleus near the base of each pair. In *Vaucheria*, however, the protoplasm of the sporangium does not break up into numerous separate zoospores, as it does in *Saprolegnia*, nor is there a second formation of zoospores.

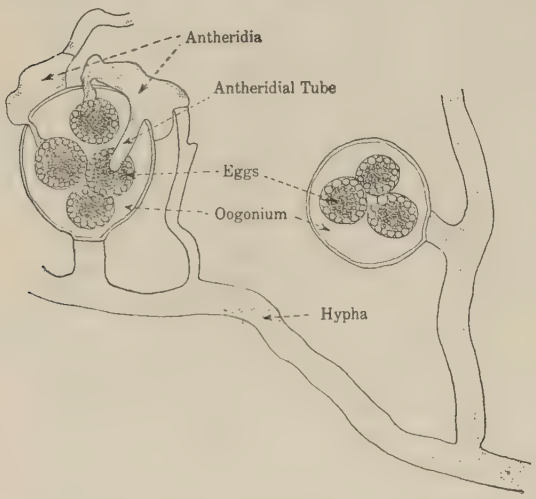


FIG. 275.—Sexual reproduction in *Saprolegnia*. (Redrawn from Sinnott in *Botany*, McGraw-Hill Book Co., Inc.)

Sexual Reproduction.—The gametangia of *Saprolegnia* also resemble those of *Vaucheria*. The oogonia may be borne either at the ends or on the sides of hyphal branches. Each oogonium is a spherical structure, the contents of which form one or more eggs (female gametes). Antheridia arise on branches near the oogonia. They are tubular in form and curve so that they come in contact with the oogonia. A slender tube is then sent out which penetrates the wall of the oogonium. The contents of the antheridium consist of several non-motile male gametes. These are discharged into the oogonium and fertilization results, after which the eggs form thick-walled oospores which upon germination form new hyphae directly.

In many cases, the eggs develop into spores without fusion with the male gamete. It will be recalled that such development of a gamete into a spore without fertilization (parthenogenesis) sometimes occurs in *Spirogyra*. This phenomenon is occasionally met with in all the great groups of plants in which sexual reproduction takes place and in many of the lower animals.

ALBUGO CANDIDA

Another representative of the Oomycetes is *Albugo candida*, which belongs to the order Peronosporales. It is a parasite, attacking members of the mustard family (Cruciferae) and causing a disease known as **white rust.** The principal sysmptom of the disease are distortions and enlargements of the flower clusters and fruits, and the development of porcelain-white blotches or blisters on the leaves and stems.

The Plant Body.— The mycelium is composed of non-septate hyphae which penetrate the tissues of the host, occupying intercellular spaces. The hyphae send out small, slender, lateral projections called **haustoria,** which penetrate the cell walls, enter the cells, become swollen at the tip, and act as absorbing organs.

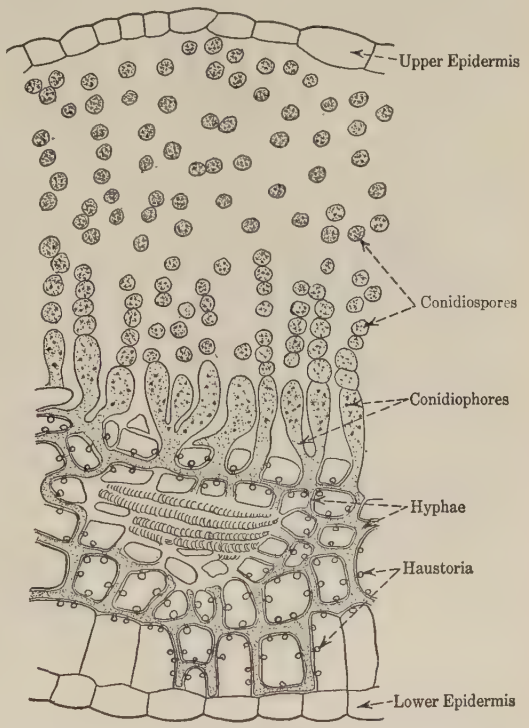


FIG. 276.—"White rust" of crucifers (*Albugo candida*) on shepherd's purse, showing the hyphae with their knob-like haustoria, the erect conidiophores, and multinucleate conidiospores. Note that by growth of the conidiophores and conidiospores the epidermis is being torn from the underlying mesophyll. (Redrawn from Chamberlain.)

Asexual Reproduction. — (See Figs. 276 and 277*A*). At certain points on the stem or leaves of the host, hyphae develop in great abundance just below the epidermis. They give rise to numerous, erect, spore-bearing branches (**conidiophores**) at the tips of which chains of spores are cut off. Asexual spores of this type, produced by constrictions of a hyphal branch, are called **conidiospores.** The growth of the conidiophores and conidiospores finally ruptures the epidermis, the conidiospores breaking off easily and being dispersed by the wind. Each conidiospore is multi-

nucleate. In the film of water which may occur on the surface of the host, the protoplasmic contents of the spore divide into numerous laterally biciliate zoospores. These escape, swim about for a while, and then come to rest and develop a germ tube which is capable of penetrating the host and starting a new mycelium

Sexual Reproduction.—(See. Fig 276*B*). The oogonia and antheridia develop on separate hyphae within the intercellular spaces of the host tissue. Within the oogonium there are numerous nuclei but one of

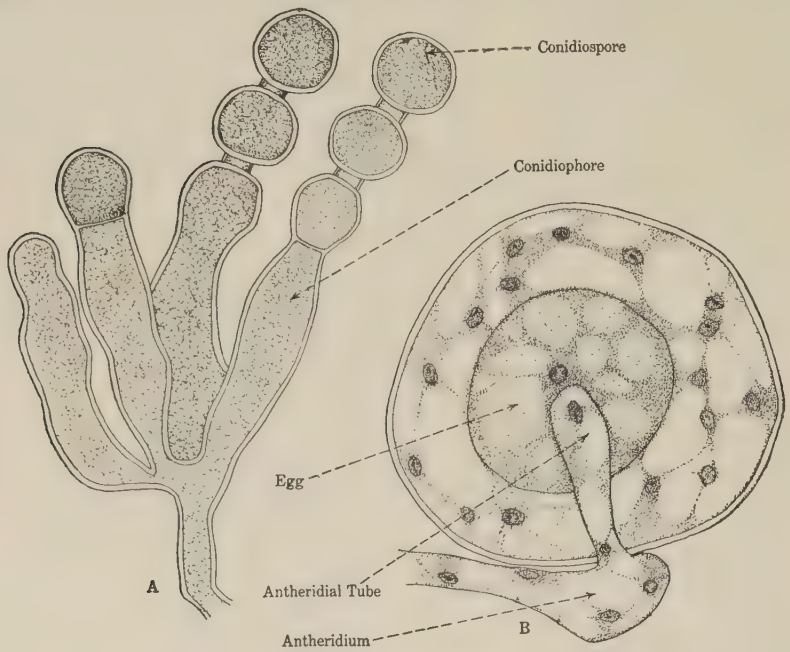


Fig. 277.—"White rust of crucifers" (*Albugo candida*). *A*, showing development of conidiospores. *B*, fertilization.

these occupies the center of the oogonium and is surrounded by a broad zone of cytoplasm which is somewhat differentiated from the multinucleate protoplasm lying outside of it. The central nucleus and the zone of cytoplasm around it constitute the female gamete.

The antheridium is an elongated cell and, like the oogonium, is multinucleate. It comes in contact with the oogonial walls, and sends out a fertilizing tube which penetrates the wall and the outer multinucleate layer of the protoplasm of the oogonium. Through this tube, a single male nucleus passes and unites with the egg nucleus. The fertilized egg nucleus, together with the surrounding cytoplasm, consti-

tutes the oospore, which develops a heavy wall about itself. It is set free by the decay of the host tissue in which it is embedded. These oospores are resting bodies; in fact it has been found that a period of rest is necessary before they are capable of germination. On germination, the oospore either develops zoospores or produces a mycelium directly.

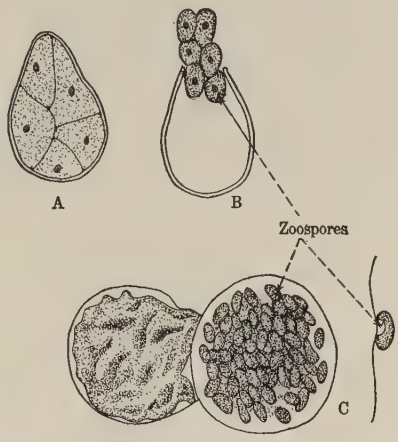


FIG. 278.—"White rust" of crucifers (*Albugo candida*). *A*, conidiospore, the protoplasmic contents of which have divided preparatory to zoospore formation. *B*, zoospores, with cilia not yet extended, escaping from conidiospore. *C*, germinating oospore discharging the numerous zoospores which for a time are surrounded by a membrane. (*C*, redrawn from de Bary.)

RHIZOPUS NIGRICANS (BREAD MOLD)

This is the best-known representative of the Zygomycetes. It is very commonly found growing on stale bread, decaying fruit and vegetables, and other organic materials left exposed to the air in moist places. *Rhizopus* spores are almost always present in the atmosphere except just after a heavy rain or snow storm when the air is almost free of bacteria and fungus spores.

If a piece of bread which has been moistened and exposed to the air is kept at a moderate temperature for a day or two in a closed dish or under a bell jar there generally develops upon it a mass of whitish mycelium. The hyphae of which this mycelium is made up develop from spores which settled from the air upon the bread and, finding there a suitable substratum, germinated.

The Plant Body.—The mycelium of bread mold consists of profusely branching coenocytic hyphae. These grow upon and within the substratum which supplies the necessary food. Certain hyphae, called stolons, of larger diameter than those which are formed within the substratum, grow just above its surface for a short distance, and then come into contact again with the substratum. At the point of contact there is produced a cluster of branches which penetrate the material upon which the fungus is growing and constitute a holdfast. Later there arise at this point a number of erect branches upon which the sporangia are produced. These groups of branched filaments suggest in their appearance the roots of the higher plants. From the base of

these another stolon grows out and this in turn comes into contact with the substratum and another holdfast and group of erect hyphae are formed. This may be repeated many times. The behavior of these horizontal hyphae suggests somewhat the formation and rooting of the runners or stolons of strawberries and other stolon-bearing plants, and on that account this fungus once bore the specific name *stolonifer* (stolon bearing).

Asexual Reproduction.—The erect hyphae arising at the points of attachment of the stolons grow away from the substratum and the tip of each of these develps into a globular **sporangium.** Hence such hyphae

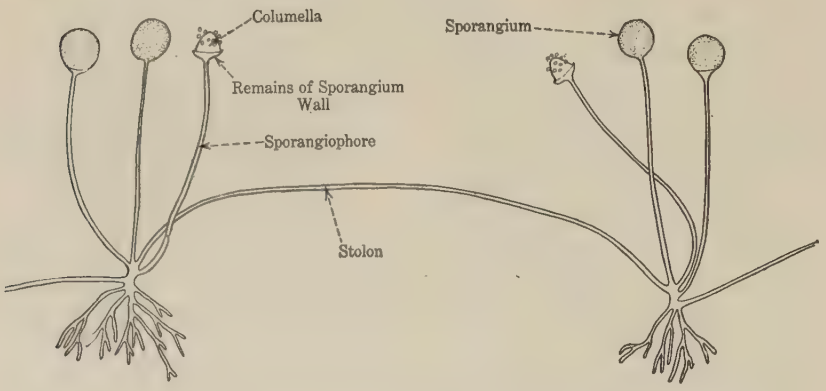


FIG. 279.—Bread mold (*Rhizopus nigricans*), showing groups of sporangiophores, rhizoid-like branches and stolons.

are called **sporangiophores** (sporangium-bearers). Several stages in the development of a sporangium are shown in Fig. 280.

As the sporangium commences its development, the tip of the sporangiophore begins to swell and in this region the protoplasm becomes more dense and the nuclei more numerous than toward the base. Gradually the protoplasmic contents of the swollen tip increase in density toward the periphery, whereas the central portion remains less dense and vacuolate. Finally a cleft is formed between the denser, peripheral protoplasm and the central protoplasm and at this cleft a wall is constructed which separates the two regions. This dome-shaped wall is called the **columella.**

During the development of the columella, the dense peripheral protoplasm breaks up into numerous angular masses, each containing several nuclei and surrounded by a cytoplasmic membrane. Each one of these multinucleate masses becomes rounded off and surrounded by a thick, black, cellulose wall, and develops into a spore. The sporangium wall

finally becomes mucilaginous, so that it readily dissolves in the presence of water, and the numerous spores are set free. It is known that these spores will retain their vitality for many years in a dry state. On the

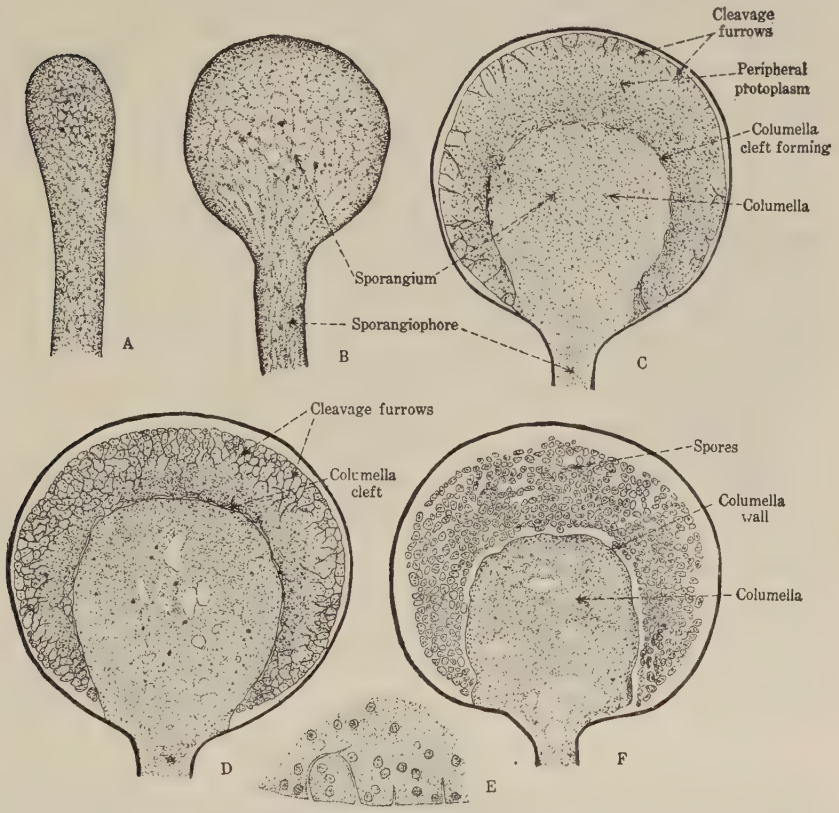


FIG. 280.—Stages in the development of the sporangia and in the formation of the spores of *Rhizopus nigricans* (common black mold) as seen in longitudinal sections. *A* and *B* show the enlargement of the free end of a sporangiophore to form the sporangium. *C*, *D* and *F* show the formation of the columella, and of the spores by furrowing of the protoplasm between the columella and the sporangium wall. *E* shows in greater detail a small portion of the cytoplasm of the sporangium represented in *C*. (Redrawn from D. B. Swingle's paper, Bureau of Plant Industry, Bulletin No. 37.)

other hand, they are capable of immediate germination, if they fall upon a suitable substratum.

Sexual Reproduction.—Sexual reproduction occurs under certain conditions, later to be described. In this process, pairs of club-shaped hyphal branches are formed which come into contact at their tips.

(See Fig. 282.) The mass of dense protoplasm in the tip of each of these branches is cut off by a cross wall. The enclosed compartments thus formed are the **gametangia** and the multinucleate protoplasm enclosed in each is a **coenogamete.** Following a dissolution of the walls of the gametangia at the point of contact, the two adjoining coenogametes fuse and, inasmuch as the two fusing masses are alike in structure, the fusion is called **conjugation.** The zygospore thus formed develops a thick black wall about itself. After a resting period, the zygospore germinates and sends out an erect hypha, at the tip of which a sporangium containing asexual spores is formed.

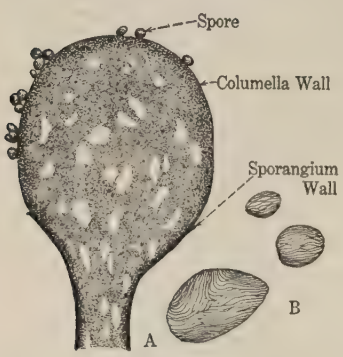


FIG. 281.—*Rhizopus nigricans* (common black mold). *A*, Columella of sporangium after the breaking of the sporangium wall. *B*, mature spores (highly magnified and showing characteristic sculpturing of wall).

It very often happens that no zygospores make their appearance in *Rhizopus* cultures even though the growth of mycelium is luxuriant, the production of asexual spores abundant, and the cultures apparently normal in every respect except for the absence of any indications of sexual reproduction. In such cases no change in the substratum, or in the conditions under which the fungus grows, will induce zygospore formation. In certain localities zygospores may not be found in *Rhizopus* cultures prepared over a period of many years, while in other localities they are formed in every culture

The reason for this peculiar condition has been made clear by the investigations of the American botanist, Blakeslee. He has shown that there are two strains or races of *Rhizopus nigricans*, the only conspicuous difference between the two being that one strain (which he calls the "+ strain") grows somewhat more vigorously than the other (the "− strain"). Sexual reproduction never takes place unless these two strains are growing together in the same culture, for hyphae of the "minus" strain can not conjugate with other hyphae of the same strain, nor can hyphae of the "plus" strain conjugate with other "plus" hyphae. In some localities only one of the strains seems to be present. The strain persists by reason of the production of asexual spores, but in such localities, zygospores will never be formed unless the strain which is lacking is introduced from some other place.

We have to do here with a slight sexual differentiation, scarcely recognizable externally but clearly apparent from the behavior of the

two strains. There are some other molds which resemble *Rhizopus* in this respect. All such species are said to be **heterothallic.** In the case of such molds, opposite strains of different species can conjugate incompletely but without zygospore formation (Fig. 283).

The zygospores of heterothallic species contain nuclear material from both strains. However, the two strains are segregated when the asexual spores are formed in the sporangium to which each zygospore gives rise when it germinates. Accordingly, part of these asexual

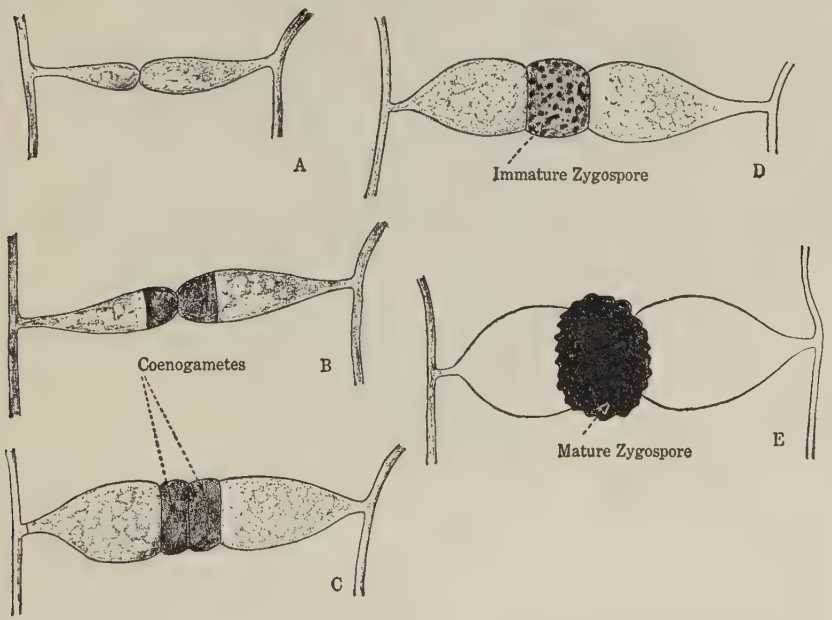


FIG. 282.—Bread mold (*Rhizopus nigricans*), showing stages in the formation of the zygospore.

spores, when they germinate, will give rise to plants of the minus strain and part to the plus strain, but none of them to plants combining the characters of the two strains. There are many molds related to *Rhizopus* which form zygospores by the conjugation of hyphae of the **same** mycelium. These are spoken of as **homothallic.**

THE DOWNY MILDEWS

The downy mildews (the family Peronosporaceae) are characterized by the development of conidiophores on the surface of the host rather than beneath the epidermis as in *Albugo*, and by the fact that the conid-

iospores are borne singly, rather than in chains. There are three common genera in the family, which cause diseases known popularly as "downy mildews." These are *Phytophthora, Plasmopara* and *Perono-*

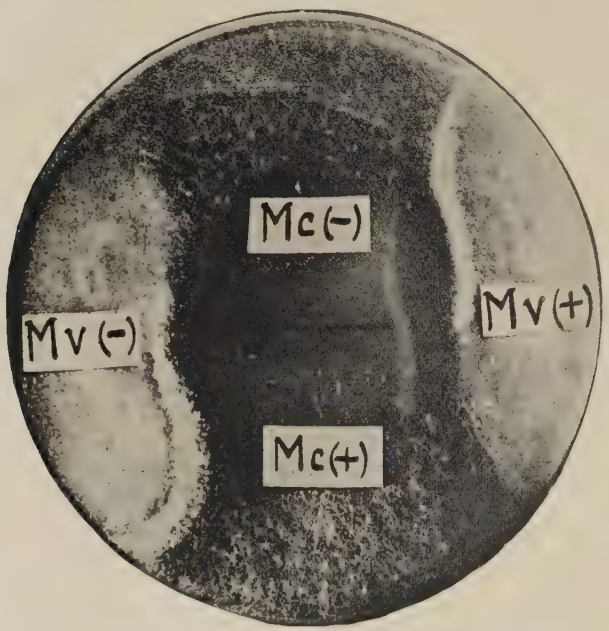


FIG. 283.—Petri dish culture of two species of mold (*Mc* and *Mv*), showing their behavior when two different strains of the same species grow together and when strains of two different species grow together. When a favorable substratum (such as nutrient agar-agar jelly or moist bread) is inoculated at one place with spores of the minus strain *Mc*(−) of a mold and at another place with spores of the plus strain *Mc*(+) of the same mold the mycelia of the two strains will grow outward from the points of inoculation over the surface of the substratum and will finally come into contact. Soon a black line will appear where the growths of the two strains have come into contact, this line resulting from formation of zygospores where the hyphae of the two strains have conjugated. If the two inoculations had been made, not with plus and minus strains of the species, but with one strain *Mc*(−) or *Mc*(+) of one species and with the opposite strain *Mv*(+) or *Mc*(−), respectively, of some other mold there generally appears a distinct white line resulting from incomplete conjugation (without zygospore formation) between the opposite strains of the two different molds. Clearly in the case of a heterothallic mold of which only one strain is known, it is possible by growing it with both strains of another mold to determine whether it is the "plus" or "minus" strain. (After Blakeslee from Gager.)

spora. *Phytophthora infestans* is the cause of the well-known potato malady known as "late blight." It is of interest to note that the serious

famine in Ireland in 1845 was largely due to the failure of the potato crop, resulting from the attacks of this fungus. The mycelium is found in the tissue of leaves, stems, and tubers and causes a wilting or blighting of the leaves and a rot of the tubers. The conidiophores, which emerge through the stomata, are branched, and at the tip of each branch a single conidiospore is borne. The conidiospores generally germinate directly, but under certain conditions their protoplasmic contents breaks up into zoospores. The disease spreads rapidly from plant to plant by means of the conidiospores and its progress may be so rapid as to devastate extended areas within a few days.

Plasmopara species are responsible for downy mildews of the grape (*Plasmopara viticola*) (Fig. 285), and of the cucumber (*Plasmopara cubensis*). As in *Phytopthora*, the conidiophores issue from the stomata and bear singly at the branch tips conidiospores each of which give rise to several lateral, biciliate zoospores. Oogonia and antheridia have been found in *Plasmopara viticola*.

In the genus *Peronospora*, the conidiospore does not produce zoospores but upon germination develops a mycelium directly. Onion mildew, caused by, *Peronospora schleideniana*, is a disease of considerable consequence in this country.

FIG. 284.—Germinating zygospore of *Rhizopus*.

PHYCOMYCETES—A SUMMARY

1. The group includes both parasitic and saprophytic forms. There are parasitic species which attack animals and others which attack plants. Various kinds of organic matter furnish a suitable food supply for the saprophytic forms.

2. The hyphae are characteristically coenocytic and non-septate.

3. Asexual reproduction is by spores, which may be non-motile as are conidiospores and the asexual spores of bread mold, or motile (zoospores) as in *Saprolegnia*. Conidiospores arise by abstriction and either occur in chains as in *Albugo* or singly at branch tips as in the downy mildews.

4. The gametes may be similar, as in the Zygomycetes, and unite

to form a zygospore; or they may be unlike as in the Oomycetes, and unite to form an oospore.

5. In the Phycomycetes a transition is noted from the aquatic to the terrestrial habit. The Oomycetes are chiefly aquatic, or at least at some portion of their life are dependent upon water for spore distribution, on account of the development of motile spores (zoospores),

Fig. 285.—Downy mildew of the grape (*Plasmopara viticola*). At the left a young cluster of Concord grape affected with the disease. At the right a healthy cluster. (From Hein, in Circular of the *Insect Pest and Plant Disease Bureau* of Nebraska.)

whereas the Zygomycetes are principally aerial and produce non-motile spores.

6. The coenocytic hyphae and the form of the sporangia and gametangia in the Oomycetes strongly suggest a relationship between the Phycomycetes and such forms as *Vauchiera*, a green alga, belonging to the Siphonales.

ASCOMYCETES

Characteristics of the Group.—The Ascomycetes is the largest group of the fungi, including a great variety of forms, over 19,000 in all, many of which are of importance on account of their causing diseases of economic plants.

The one outstanding characteristic of the group, and the one that suggested the name Ascomycetes, is the formation, somewhere in the life history, of sac-like hyphae called **asci** (singular **ascus**) within each of which are produced a number of spores (generally eight), called **ascospores.** In addition to ascospores, conidiospores are also produced by many Ascomycetes. The hyphae of Ascomycetes differ from the coenocytic hyphae of the Phycomycetes in being septate, that is, divided by traverse walls into cells, each of which may contain one or more nuclei.

In *Exoascus*, which is parasitic on plums, peaches and other related plants, causing a leaf curl and enlarged hollow fruits, the asci are not enclosed but are produced at the surface of the infected organ (Fig. 287). In most Ascomycetes the asci are produced in special, often large and fleshy, fruiting bodies, called **ascocarps.** In *Peziza* and *Sclerotinia*, the asci are borne in a cup-shaped or saucer-shaped ascocarp, which is called an **apothecium.** In the powdery mildews, the asci are formed within a more or less spherical ascocarp, called a **perithecium,** which is entirely closed. Thus ascocarps are either apothecia or perithecia.

Fig. 286.—Leaf curl of peach caused by *Exoascus deformans.* At the left, branch with diseased leaves. At the right, healthy branch. (From Annual Report of the New Jersey Agricultural Experiment Station for 1913.)

In addition to many important parasitic Ascomycetes causing plant diseases, the group also includes such non-parasitic forms of economic importance as the blue and green molds, so common on preserves and decaying fruit, the yeasts and the truffles.

PEZIZA

One of the most common saprophytic Ascomycetes is *Peziza*, which belongs to the sub-class Discomycetes, one of the largest groups of the ascus fungi.

Plant Body.—The mycelium of the various species of *Peziza* generally grows in soil very rich in organic matter or in decaying wood. There arises from the mycelium a conspicuous ascocarp which is in the form of a cup and often has a brightly colored lining. In one species, *Peziza aurantiaca*, the inside surface of the cup is bright red. A section through the **hymenium** (tissue lining the interior of the cup) shows numerous cylindrical asci each containing eight ascopores, and intermixed with the asci numerous sterile branches or hyphae known as **paraphyses.** The asci and paraphyses are perpendicular to the surface of the hymenium and parallel to each other.

Reproduction.—Although no gametangia have been found in *Peziza*, they have been discovered and carefully studied in the closely related form, *Pyronema.* In this the mycelium gives rise to female and male gametangia which are produced in close proximity. The oogonium consists of a globular cell with a long tubular outgrowth which greatly resembles the trichogyne of certain red algae, such as *Nemalion.* The oogonium is multinucleate. The antheridium is a cylindrical terminal cell, also multinucleate, which arises below the oogonium. The tubular trichogyne curves toward the antheridium and their tips come together; the intervening walls are broken down and the contents of the antheridium move into the trichogyne and downward into the oogonium. A union of male and female coenogametes ensues. The fertilized oogonium sends out a number of hyphae, at the tips of which the asci are developed. The asci are intermingled with paraphyses which arise from beneath the oogonium. Other sterile hyphae form the cup-shaped ascocarp. In such forms as *Peziza* and *Pyronema* the spores are discharged from the asci in great numbers and scattered over considerable distances by air movements.

SCLEROTINIA

This genus somewhat resembles *Peziza*, and includes several species of great economic importance. Well-known diseases caused by species of *Sclerotinia* are brown rot of stone fruits, lettuce drop and stem rot of clover. The most destructive of these is the first-mentioned disease which injures twigs, flowers and especially fruits. The first evidence of the disease noticeable on the fruit are small, dark brown spots, which enlarge and cover the entire fruit. Then the fungus breaks through to the surface, forming small brown tufts which close examination shows to be composed of numerous conidiophores bearing conidiospores. These spores are light in weight and are carried by the wind to other fruits, where they may germinate at once and infect the fruits. The

apothecial stage is observed on shriveled or mummified fruits. The apothecia are cup-shaped and arise from a compact mycelial mass, called a **sclerotium,** which develops either on or within the tissues of the dried-up fruit. Asci and paraphyses arise from the inner lining of the apothecium. Conidiospores and ascospores may cause infection of healthy trees.

Fig. 287.—Section of peach leaf affected with leaf curl which is caused by *Exoascus deformans*. Asci containing ascospores are forming on the upper surface of the leaf; *a*, leaf cuticle; *b*, hyphae; *c*, young asci with spores not yet formed; *d*, spores just formed; *e*, smaller spores formed by the budding of the ascospores; *f*, spores discharging; *g*, empty ascus. (After Swingle in Montana Agricultural Experiment Station Bulletin.)

POWDERY MILDEWS

The powdery mildews belong to a large family of Ascomycetes all of which are strictly parasitic and produce their mycelium on the surface of the host. The hyphae bear haustoria, which penetrate the host cells. Asexual spores of the conidial type are produced, and asci are developed in perithecia.

The conidiospores are produced in chains on the surface of the host, often in such tremendous numbers as to give a mealy or powdery appearance to the diseased structures and to suggest the name "powdery mildew." The conidiospores may germinate immediately after they are shed and thus the disease may spread rapidly from plant to plant.

Following the production of conidiospores the mycelium may form perithecia which are developed on the surface of the host plant. When

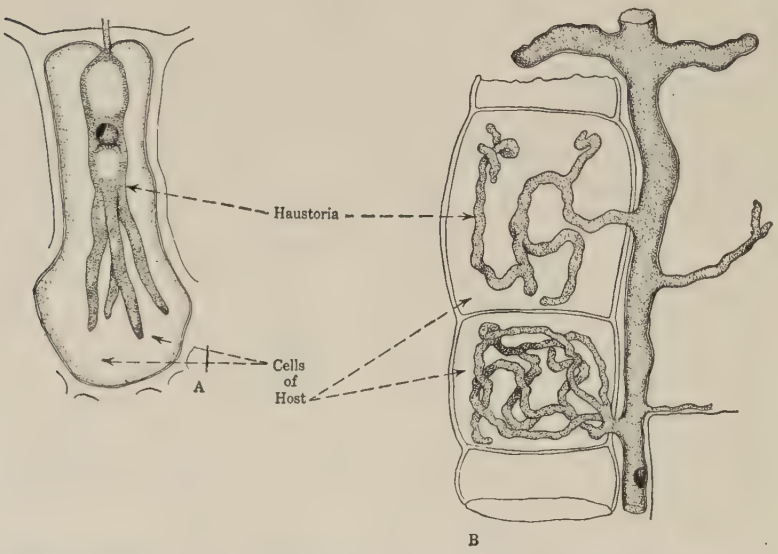


FIG. 288.—Haustoria of (*A*) a powdery mildew fungus (*Erysiphe graminis*) and *B* a downy mildew fungus (*Peronospora*). *A* after C. C. Curtis, *B* after Smith.

mature they may be seen with the naked eye as black specks in a cobwebby mycelial growth. Stages in the development of the perithecia are shown in Fig. 290. Two adjacent hyphae give rise to erect branches, which are unequal in size. A tip cell containing a single nucleus is cut off by a cross wall in each branch. The apical cell of the larger branch is the oogonium, and that of the smaller branch is the antheridium. These gametangia come in contact, there is a dissolution of a part of the wall separating the two, and the nucleus of the antheridium enters the oogonium and fuses with its nucleus. From the fertilized oogonium there are formed more or less indirectly one or more asci. Sterile hyphae growing out from a cell beneath the oogonium finally

completely surround the ascus or asci to form a characteristic perithecium. In some powdery mildews, such as *Sphaerotheca* and *Podosphaera*, a single ascus is borne in each perithecium; in others, as *Erysiphe*, *Microsphaera*, *Uncinula* and *Phyllactinia*, the perithecia contain more than one ascus. The perithecium often bears characteristic appendages, which are much used in the classification of these filaments.

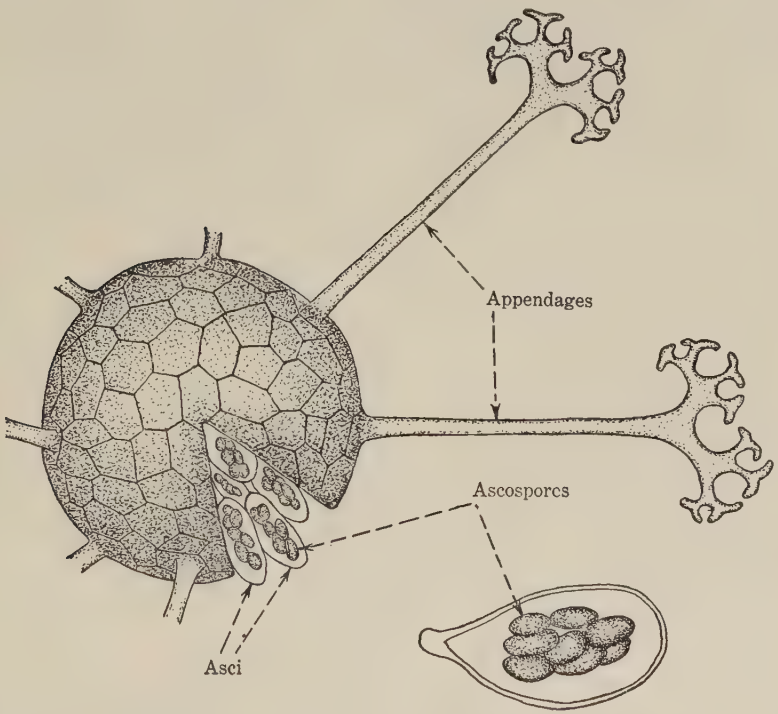


Fig. 289.—Powdery mildew of lilac, *Microsphaera alni*. Mature ascocarp, and at right a single ascus.

For example, in the genera *Sphaerotheca* and *Erysiphe*, the appendages are simple, flexuous and undivided at the tip; in *Podosphaera* and *Microsphaera*, they are dichotomously branched; in *Uncinula*, they are spirally rolled at the tip; and in *Phyllactinia*, they are swollen at the base.

BLUE AND GREEN MOLDS

These are well-known saprophytic ascomycetes found on a great variety of substances. *Aspergillus* and *Penicillium* are the two most common genera, and each has a number of species. *Aspergillus* species

occur on decaying vegetables of all sorts, on moldy cereals, on jellies, old leather, paper, ensilage, etc. The mycelium produced is prolific and spores arise in tremendous numbers. Spores are developed on conidiophores, and arise by abstriction of terminal branches. The

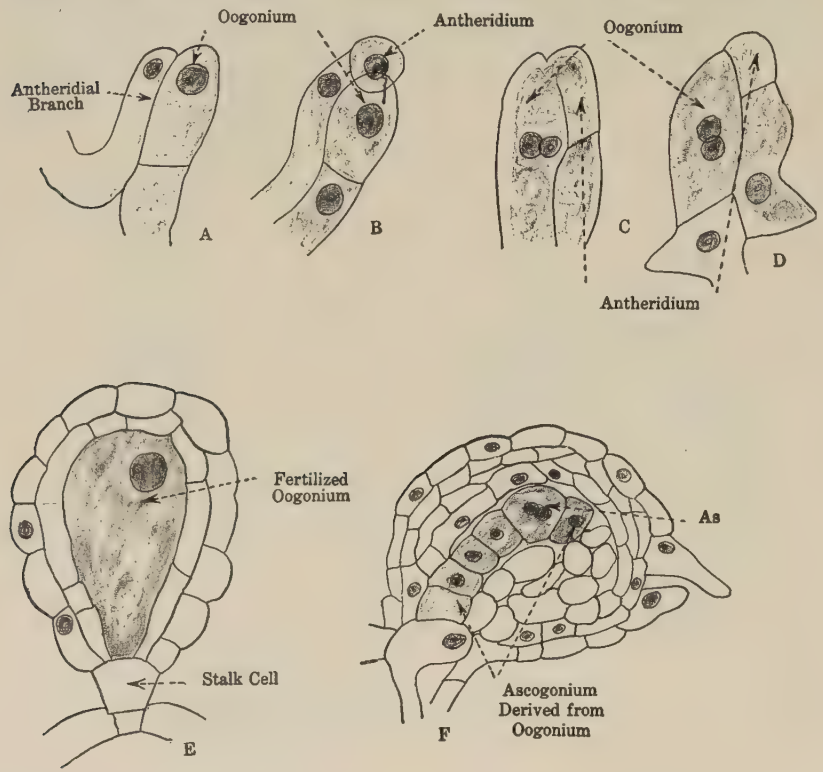


FIG. 290.—Stages in the development of a perithecium of a powdery mildew. *A*, antheridial and oogonial branches in contact. In *B* the antheridium and oogonium are cut off from the tips of the branches; *C*, movement of antheridial nucleus toward nucleus of oogonium; *D*, union of male and female nuclei. *E*, fertilized oogonium surrounded by hyphae derived from a cell just below the oogonium (stalk cell); *F*, multicellular ascogonium; *As*, cell which gives rise to the ascus. (Redrawn from Harper.)

characteristic color of the mold appears when the conidiospores develop; in the different species they are various shades of green, brown, yellow and red. The conidiospores, which are carried by air currents, and when in abundance impart a characteristic moldy odor to the atmosphere, are capable of immediate germination if they fall upon the proper substratum.

Of the numerous species of *Aspergillus*, perithecia are known in only a few. The perithecium develops from two short hyphae which

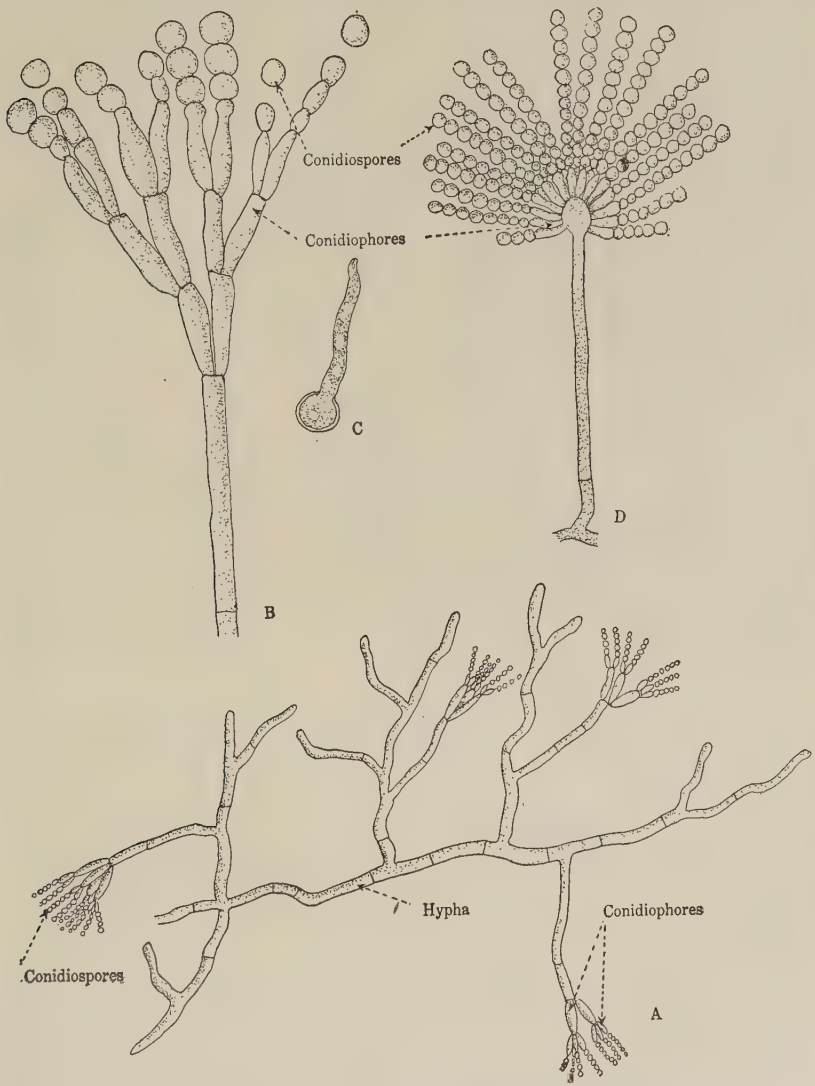


FIG. 291.—Blue and green molds. *A* and *B*, common blue mold (*Penicillium*). *C*, germinating conidiospore. *D*, green mold (*Aspergillus*).

are spirally coiled about each other. Each of these hyphae consists of several cells. One of the hyphae is regarded as the oogonium; and the

other as the antheridium. The fusion cell formed after a dissolution of the separating walls gives rise to hyphae which bear asci, each of which contains eight ascospores. The ascus-bearing hyphae become surrounded by other highly branching, sterile hyphae which completely enclose them and form a perithecial wall.

Penicillium is the common blue mold on bread, cheese, lemons, etc. The conidiophores are branched, each branch bearing a chain of conidiospores. Sexual reproduction has been observed in several species of *Penicillium*, the process being very similar to that of *Aspergillus*.

Several species of *Penicillium* are of importance in the manufacture of certain kinds of cheese. For example *Penicillium Roqueforti* is the active agent in the ripening of Roquefort, Gorgonzola, and Stilton cheeses, and *Penicillium Camembertii* in the case of Camembert cheese.

YEASTS

The position which the yeasts occupy in relation to other plants has long been a subject of debate. Usually, however, they are included with the Ascomycetes because of their production, under certain conditions, of structures which somewhat resemble asci.

The beer, alcohol and wine yeasts are included in the genus *Saccharomyces*, which has a number of species. *Saccharomyces cerevisiae* is by far the most important species, being the one employed in beer-brewing and bread-making.

Yeast cells may remain attached to form a short chain but they do not produce a true mycelium. The cells are usually egg-shaped or spherical and each cell is surrounded by a well-defined wall. Within the yeast cell may be discerned the nucleus, oil globules and vacuoles. One of the chief characteristics of the yeasts is their method of vegetative reproduction by "budding." In this process, a portion of the protoplasm of a cell forms a lateral outgrowth (bud) surrounded by a cell wall which finally may separate to form a new individual.

Ascospores are produced only when there is an abundance of oxygen. In the production of ascospores the cell nucleus divides into several daughter nuclei, each one of which becomes the center of a spore lying within the original cell. The number of spores developed in a single yeast cell varies, but it is usually four. On disintegration of the wall of the original cell, the spores are liberated, and under proper conditions produce new yeast plants.

Fermentation.—The most important property of yeasts is that of producing alcoholic fermentation. The yeast cells absorb sugar, and within the protoplast this sugar is decomposed with the formation of

carbon dioxide and ethyl alcohol. The sugars susceptible of alcoholic fermentation by yeast are the **hexose** sugars, glucose, fructose, mannose, and galactose. The chemical action which takes place in fermentation of hexose sugar may be expressed as follows:

$$\underset{\text{glucose}}{C_6H_{12}O_6} \rightarrow \underset{\text{alcohol}}{2C_2H_5OH} + \underset{\text{carbon dioxide}}{2CO_2}$$

In the account of bacteria under the heading of carbohydrate fermentation (page 398) this transformation of certain sugars to alcohol and carbon dioxide was discussed.

The great economic importance of yeast is realized when we understand that on account of its power of producing a sugar-fermenting enzyme, it is indispensable in the making of bread, in the manufacture of commercial ethyl alcohol, and in the production of alcohol in fermented liquids used as beverages.

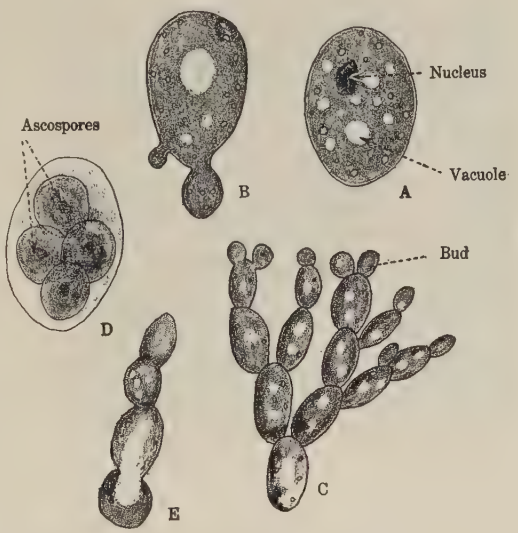


FIG. 292.—Yeast (*Saccharomyces cerevisiae*). *A*, single cell highly magnified. *B*, cell in process of budding. *C*, chain of cells formed as result of rapid budding and growth. *D*, formation of ascospores. *E*, germination of ascospore and the development of new plants by budding. (Redrawn from Curtis.)

In bread making, yeast plants are mixed with a mixture of flour and water. The flour contains some sugar in addition to the starch. At a suitable temperature, the yeast cells multiply rapidly. Zymase is formed, and breaks down the sugar into alcohol and carbon dioxide. The bubbles of carbon dioxide gas are prevented from escaping by the dough, which, however, is caused to rise by the expansion of the bubbles. At baking temperatures, there is further expansion of the gas bubbles, and also a driving off of alcohol and water.

LICHENS

General Characteristics and Distribution.—The lichens constitute one of the most extraordinary groups of plants to be found in the plant kingdom. The plant body is made up of a fungus growing in intimate relationship with an alga. The fungus forms the greater bulk of the plant body, and is usually one of the Ascomycetes, as is evidenced by the fact that it reproduces by ascospores produced in an apothecium. The alga in this plant complex belongs either to the Cyanophyceae or Protococcales. In some cases it is possible to make separate cultures of the alga and fungus which constitute the lichen, and then to bring them together and produce a lichen experimentally, the fungal threads enclosing the algal cells and forming a typical lichen body.

Fig. 293.—A crustaceous lichen.

The co-partnership of the alga and the fungus in a lichen is an excellent example of symbiosis. The manufacture of food can be carried on only by the alga, and necessarily the fungus is dependent upon the alga, from which it absorbs food. However, the alga also derives some benefit from the presence of the fungus. The fungus absorbs water from the substratum upon which the lichen lives and also from fog and moist air, and passes it on to the alga. The fungus also protects the algal cells from fatal drying out when the air humidity is very low. It should be emphasized that in a lichen two definite species—an alga and a fungus—when grown together may produce a characteristic plant body which is different in form and appearance from either component grown separately. To this compound organism we must also give a generic and a specific name.

Lichens are world wide in their distribution. They are found in a great variety of situations, and are of many different forms and colors. Crustaceous and leaflike forms occur on the surface of rocks, on the bark of trees and on the soil. Some lichens, such as the so-called reindeer moss (*Cladonia*) of arctic tundras, and *Usnea*, which is pendent from the branches of trees, grow to a large size. In many habitats

lichens are exposed to the greatest extremes of temperature and humidity. In fact they are able to live in habitats—exposed rocks and tree bark, for example—where few other plants can maintain themselves. They will undergo extreme desiccation for a long period, and revive when favorable conditions recur.

A few lichens are of some economic importance. Various pigments, including litmus, are manufactured from lichens, and some lichens are used for food by man and domestic animals. Reindeer and caribou on the northern tundras live in certain seasons, largely on "reindeer moss" (not a moss but a lichen). Lichens are also important agencies in the disintegration of rock upon which they grow.

Structure of Lichen Body.—The lichen body is a thallus, which in cross section is seen to possess an upper and a lower layer of fungal threads, between which is a region of looser hyphae. The algal cells may be scattered among the hyphae throughout the plant body, or as is more frequent, in a layer near the upper surface. Hyphae from the lower surface may act as absorbing and anchoring structures.

Reproduction.—In discussing reproduction of lichens it is necessary to distinguish between (1) the reproduction of the lichen as such, and (2) the reproduction of each of the two component organisms which make up the lichen.

In the case of many lichens, especially pendent forms like *Usnea* and *Ramalina*, there is often considerable multiplication resulting from the tearing loose by the wind of relatively large fragments of thallus which may find lodgment in places favorable for their development into large thalli. In addition most lichens form special reproductive bodies called **soredia**, each of which consists of a few algal cells surrounded by fungous hyphae. They are produced in powdery or granular masses on the surface of the thallus or in some cases on special branches. When they fall from the lichen or are carried away by the wind they may develop into lichen thalli.

The algal component consists usually of simple unicellular plants, which reproduce within the body of the lichen by fission and thus increase in number as the thallus grows. The fungal component if, as in most cases, it is an Ascomycete, reproduces by means of ascospores. These are generally borne in apothecia which are very similar to those of *Peziza* and related Ascomycetes. Unless the ascospores germinate in close proximity to cells of the algal component, a new lichen will not be formed. A few lichens produce their asci within closed ascocarps (perithecia) which open by a small pore when the ascospores have reached maturity.

In certain species the ascocarps are formed as the result of a sexual

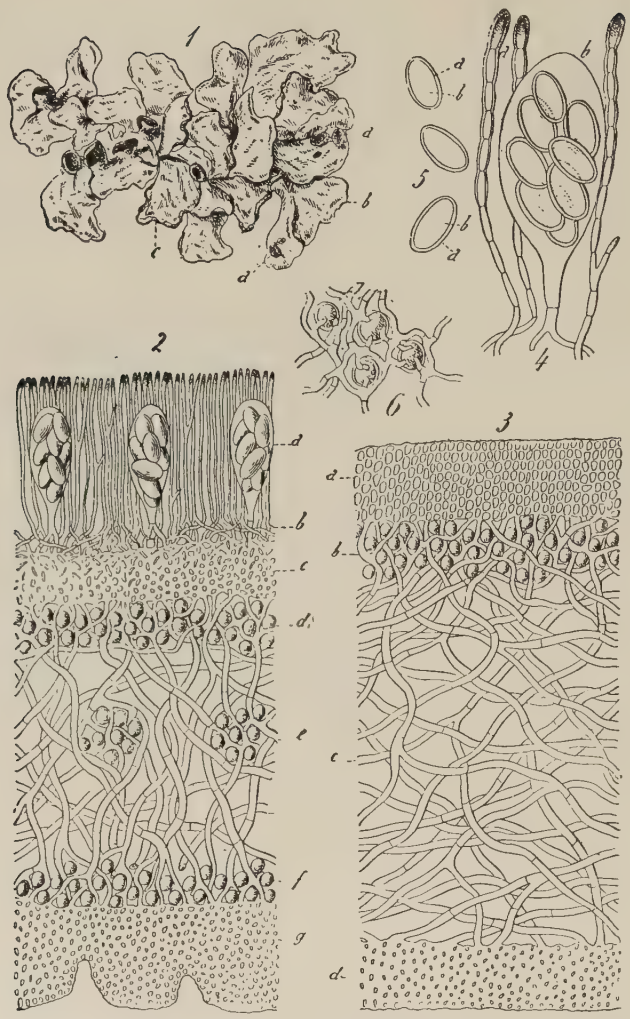


FIG. 294.—A lichen, *Parmelia perlata*. 1, Plant, slightly reduced; *a*, apothecia; *b*, lobe of thallus; *c*, soredia. 2, Longitudinal section of apothecium; *a*, asci and paraphyses; *b* and *c*, two layers of the hypothecium; *d*, upper algal layer; *e*, colonies of algae scattered among the hyphae; *f*, lower algal layer; *g*, lower cortical layer. 3, Cross section of vegetative portion of thallus. 4, Three paraphyses and a single ascocarp. 5, Ascospores. 6, Algal cell surrounded by fungal hyphae with haustoria. (After Schneider, from Gager.)

reproductive process strikingly similar to that of certain Rhodophyceae. In other cases careful study has failed to show any evidence of a sexual process.

ASCOMYCETES—A SUMMARY

1. The group includes both parasitic and saprophytic forms. Organic matter of either plant or animal origin may be a source of food. Many of the representatives cause important diseases of cultivated plants.
2. The hyphae are septate, but each of the compartments thus formed may contain several nuclei.
3. In many cases conidiospores are produced.
4. In addition, characteristic spores (ascospores) are produced in an ascus (sac); in many cases sexual fusions are known to be involved in the processes leading up to the formation of an ascus or group of asci.
5. The asci are generally produced in fruiting bodies, known as **ascocarps,** which may be open (apothecia) or closed (perithecia).
6. There is a close similarity between the Ascomycetes and certain of the Rhodophyceae as regards the structure of the gametangia and the behavior of the zygote. This likeness suggests a relationship between the two groups.

BASIDIOMYCETES (BASIDIUM-FORMING FUNGI)

Characteristics of Group.—Thus far in our discussion of fungi we have dealt with the four classes: Bacteria (fission fungi), Myxomycetes (slime fungi), Phycomycetes (algal fungi) and Ascomycetes (sac fungi). There remains for us to consider one very important class of fungi, the Basidiomycetes. The class name is descriptive of the outstanding character of the group, which is the occurrence of a special type of conidiophore, called a **basidium** (plural **basidia**), in the life cycle of these plants. It is a club-shaped hypha which produces asexual spores (**basidiospores**) singly at the end of several (usually four) slender, pointed protuberances called **sterigmata** (singular **sterigma**). In some Basidiomycetes the basidium is divided by cross walls into a number of cells (generally four) but in other forms it is non-septate.

The class Basidiomycetes is sub-divided into the following three groups:

1. Hemibasidiomycetes—the smut fungi.
2. Protobasidiomycetes—the rust fungi.
3. Eubasidiomycetes—the fleshy and woody fungi.

HEMIBASIDIOMYCETES (SMUT FUNGI)

The smut fungi are regarded as the most primitive of the Basidiomycetes. All are parasites, occurring on a wide range of hosts, the most common hosts being the Gramineae, which include the grasses, and common cereals. The smuts annually destroy millions of dollars' worth of corn, oats, barley, wheat, rye and other cereals. According to data collected, the estimated reduction of yield of cereals in the United States during 1921 due to smuts was 160,738,000 bushels.

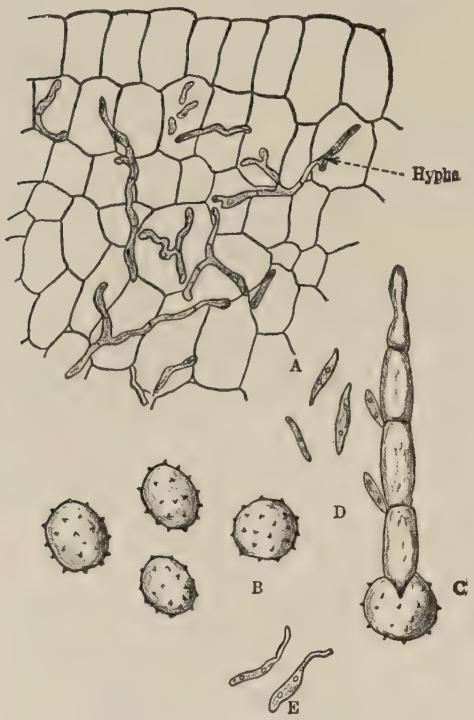


FIG. 295.—Corn smut (*Ustilago maydis*). *A*, hyphae in the tissue of the host. *B*, mature chlamydospores. *C*, a germinating chlamydospore, showing the 4-celled basidium, two cells of which are producing sporidia (basidiospores). *D*, sporidia. *E*, budding sporidia. (Redrawn from Freeman and Stakman, in Minnesota Agricultural Experiment Station Bulletin.)

Corn Smut.—The smut of corn (*Ustilago maydis*) may be selected as a type form. The mycelium of the fungus may be found in any part of the host (Fig. 295). It causes abnormalities and swellings, sometimes of considerable size. These result from the abundant development of hyphae in the tissue of the host and further from the stimulation of the tissue of the affected organ to abnormally active growth. Later, practically all of the internal tissue of the diseased part of the host is used up by the growth of the smut hyphae, so that the whole deformed structure, except the surface layer, becomes a mass of fungal hyphae. These hyphae are then transformed into millions of black spores known as **chlamydospores.** Each of these spores is formed from a short segment of a hypha which becomes surrounded by a slightly thickened wall and then separated from the adjoining segments of the same hypha. Chlamyd-

ospores are capable of germination as soon as mature if conditions are favorable, or they may retain their vitality throughout the winter and germinate the next spring. Each germinating chlamydospore produces a short hypha, called a promycelium or basidium, which is divided by cross walls into three or four cells. Each of these cells bears a single basidiospore which is generally spoken of as a **sporidium.** The sporidia are capable of multiplication by budding, such budding often going on rapidly in barnyard manure. The sporidia are readily carried by the wind and may, if they fall upon any young tissue of a corn plant, send out short hyphae which will penetrate the epidermal cells and thus infect the plant.

Fig. 296.—Wheat heads affected by bunt or stinking smut of wheat which is caused by *Tilletia.* The kernels alone are affected, each kernel being transformed into a smut ball, which is a rather compact mass of spores. (After Leach, in Colorado Agricultural Experiment Station Bulletin.)

It has been demonstrated in the case of corn smut that any part of the plant may be infected, and at any time throughout the growing season. If the young corn plant is infected in the spring or early summer, the mycelium of the parasite develops along with the growing host plant, so that as new host tissue is formed it may be invaded promptly by hyphae. For a long time there may be no evidence, other than reduced growth, that the corn plant is infected. Later, the large tumors or pustules are formed, which break open and form black, sooty masses. These "smut balls" may occur on any part of the plant above ground, but most commonly involve the ear or tassel.

Modes of Infection in Smuts.—Among the cereal smuts, three modes of infection are recognized, namely (1) **seedling infection,** (2) **flower infection,** (3) **general infection.** In seedling infection, as illustrated by bunt (stinking smut) of wheat, covered smut of barley and all oats smuts, kernel smut of sorghums, and millet smuts, the spores adhere

FIG. 297.—*A*, kernels of normal wheat, and *B*, kernels of wheat infected with bunt (*Tilletia*). The latter filled with chlamydospores of the parasite. (After Leach, in Colorado Agricultural Experiment Station Bulletin.)

FIG. 298.—Smutted oats. At the left, head affected by loose smut (*Ustilago avenae*); at the right, head affected by closed smut (*Ustilago levis*). (From Colorado Agricultural College Extension Service Bulletin.)

to the surface of the seed. When the seed germinates, the smut spores also germinate, and the smut hyphae penetrate the tissue of the seedling at once. The parasite keeps pace with the developing plant, becoming conspicuous as black, sooty masses of spores which partially or totally replace the flowering head. A smut of this sort may be held in control by treating the seed with a substance such as copper sulphate, copper carbonate or formaldehyde, which will destroy adhering smut spores, but will not injure the embryo.

The loose smuts of wheats and barley infect their hosts through the flower, the spores being incapable of infecting any part of the plant except the ovary. There is a slight development of the mycelium in the embryo of the grain and there is no apparent injury to the grain. However, when the seed germinates, the dormant mycelium begins to grow, and as the young plant develops, the mycelium keeps pace with its host. It is possible by careful microscopic study to detect the hyphae of the smuts in the stem growing point of the host (Fig. 299). Not until the flower head is forming does the presence of the parasite become evident. Then the host tissues which are infected are replaced by a mass of black spores. These are readily scattered by the wind and may infect flowers in a less advanced stage of development.

FIG. 299.—Portion of the tip of an infected barley stem showing hyphae of loose smut of barley in the tissue. (Redrawn after Freeman and Stakman, in Minnesota Agricultural Experiment Station Bulletin.)

It is obvious that the ordinary seed treatment which has for its object the destruction of smut spores adhering to the seed would be useless in controlling smuts which have infected the flowers of the host, for in smuts of this type the hyphae are within the embryo. However, a hot-water method of seed treatment has been devised which will destroy the dormant mycelium but leave the embryo uninjured.

Corn smut is an example of the third, or general, type of infection. In this, young tissue of stem, leaves, flowers, and even roots may be

infected. Since the parasite may gain entrance through any part of the plant, it is clear that seed treatment would be useless. Control of corn smut may be accomplished by removal from the field and burning of smut masses before they discharge the spores, and by a proper system of crop rotation.

PROTOBASIDIOMYCETES (RUST FUNGI)

The rusts are a group of fungi of great economic importance. They are parasites on a great variety of hosts, chiefly seed plants. Well-known diseases of economic plants which are caused by rusts are black stem rust of wheat, oats, barley and rye, asparagus rust, apple rust, orange rust of raspberry and blackberry, and blister rust of pines. The grain losses due to the black stem rust of cereals are sometimes enormous. Many epidemics of this disease have occurred, those of 1904 and 1916 in this country having been particularly destructive. According to one of the principal American authorities on cereal rusts, "the most conservative estimate places the loss of wheat in the United States due to the black stem rust in 1916 at 180,000,000 bushels, while the loss in Canada was estimated at about 100,000,000 bushels."

The rust fungi are striking examples of obligate parasites, that is, organisms which are unable to live except on living tissue. They are incapable of living in culture media, even when these media are made from the host plant upon which they thrive.

The mycelium of rusts is composed of septate hyphae which nearly always grow in the intercellular spaces of the host tissue and are branched and provided with haustoria. Spores are usually produced in patches, called **sori** (singular **sorus**), on the surface of the host. Five different types of spores may be formed in rust fungi, but all are not present in every species. These different forms of spores will be described in a later paragraph.

One of the best-known genera among the rusts is *Puccinia*. It has a number of very important species, chief of which is *Puccinia graminis*, the black stem rust of wheat, oats, barley, rye, and many grasses.

LIFE HISTORY OF PUCCINIA GRAMINIS (BLACK STEM RUST)

Red-spore Stage.—The first visible evidence of this rust on cereals is seen on the stems and leaves as reddish-brown streaks or pustules, which make their appearance in the spring and summer. These are caused by groups (sori) of minute yellowish spores formed just beneath the epidermis of the host. These spores are known as **uredospores,** and the sori as **uredosori.** These spores are external evidence of the presence of a mycelium growing between the cells of the tissues of the host. The production of these spores is spoken of as the " red rust " stage of the disease. The mycelium which gives rise to the spores is intercellular and forms haustoria which penetrate the cells and absorb foods from the living protoplasts. Each uredospore is stalked, one-celled and ovate, and has a rather thick wall which bears numerous small spiny projections. These spores are disseminated by the wind. They are capable of germination within four or five days after they are shed, if sufficient moisture is present. Infection takes place by the growth of the germ tube through a stoma into the host tissue. (Fig. 303.) Within the host tissues this hypha branches and forms a new mycelial growth. Within a short time the mycelium absorbs sufficient food from the host to form a new crop of uredospores. Thus it is possible to have a number of successive crops of uredospores in a season, and from one or a few infected plants the disease may spread over a large area. In fact, the red stage may thus repeat itself under favorable environmental conditions every seven to ten days. The epidemics of rust in grain districts are chiefly due to weather conditions which favor the development of successive crops of red rust spores, and thus make possible the rapid spread of the disease.

Black-spore Stage.—Usually in the late summer or fall when the grain begins to ripen, black pustules or sori appear on the same culms and leaves which produced the uredosori. These black sori consist of dark-colored spores known as **teleutospores.** The sori are called **teleutosori.** One may sometimes find both uredospores and teleutospores in a single sorus. The teleutospores are stalked, two-celled structures, which are spindle-shaped and have a thick wall. They are unable to germinate at once as do the uredospores, but after wintering in the open on stubble or on the soil, they germinate freely.

The Sporidium Stage.—At germination, one or both cells of the teleutospore may send out a tube, which, as in the smuts, is called a promycelium or basidium. This is generally a four-celled structure, each cell of which forms a single colorless **sporidium** (**basidiospore**) on a short **sterigma.** The basidiospores are carried by the wind. They

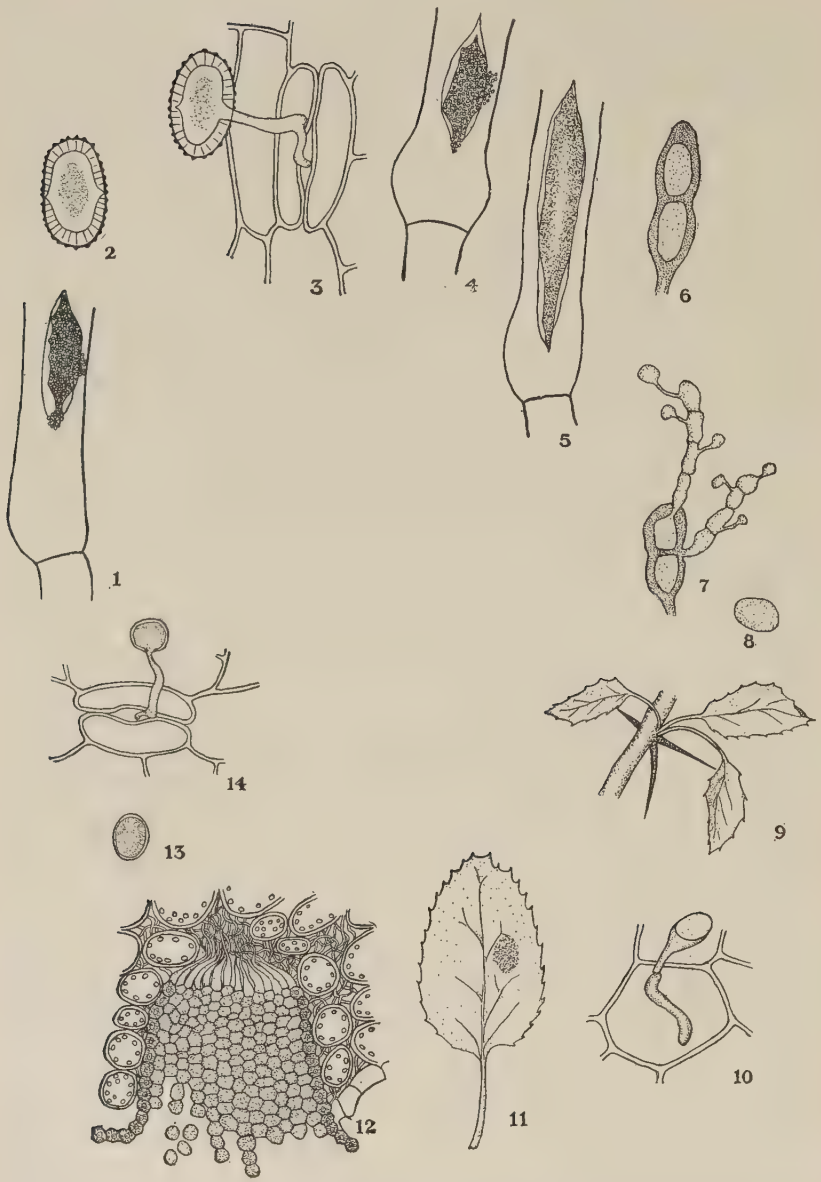


FIG. 300.—Life cycle of black stem rust (*Puccinia graminis*)—an heteroecious rust. 1, Uredosorus on wheat stem. The red uredospores which are produced early in the season are known as summer spores. 2, A single uredospore. 3, Germinating uredospore on surface of the stem of another wheat plant, its germ tube penetrating a stoma. As a result a mycelium is formed within the tissues of the

Continuation of the legend on the next page.

will not germinate unless they fall upon the leaves, twigs, or fruit of certain species of the barberry, the most important of which is the common barberry (*Berberis vulgaris*). Here a germ tube is formed which penetrates the tissues of the plant, entering through a stoma.

The Spermagonial and Aecidial Stages.—Within seven to ten days after the barberry plants are infected by basidiospores, there appear submerged below the surface on the upper side of the leaves small flask-shaped bodies which break through the epidermis. Somewhat later, clusters of yellowish cups are found on the lower surface of the leaf.

The small flasked-shaped bodies are known as **spermagonia.** Within them are produced rod-shaped or oval spermatia. These latter bodies apparently do not function in the life history of the fungus. The cup-shaped structures are called **cluster-cups** or **aecidia.** At maturity these are filled with chains of yellowish one-celled spores, known as **aecidiospores.** The aecidiospores are scattered by the wind and may infect the proper grass host. A mycelium is developed within the tissues of the grass plant, and gives rise to uredospores.

Spore Forms.—In black rust of cereals, just described, there are five spore forms, as follows:

1. *Uredospores*—in sori on the grass host.
2. *Teleutospores*—in sori on the grass host.
3. *Sporidia* (basidiospores)—on a promycelium or basidium developed directly from the germinating teleutospores on the soil or stubble.
4. *Pycniospores* (Spermatia)—in pycnidia (spermagonia) which open on to the surface of the barberry leaf. These are apparently functionless. They may formerly have functioned as male gametes.

host and soon another crop of uredospores is borne in uredosori as shown in (4). Thus during a single season there may be many successive crops of uredospores, the disease thus spreading rapidly over a field. 5, A teleutosorus produced later on wheat stems. The dark teleutospores which are liberated from the sorus are known as winter spores. They remain alive on the straw during the winter. 6, A single teleutospore. 7, A teleutospore germinating the spring following its formation. Each cell is sending out a 4-celled promycelium (basidium) each cell of which may produce one sporidium (basidiospore). 8, A single sporidium. If the sporidia fall upon a common barberry leaf (9), they germinate as shown in (10), and the germ tube penetrates the leaf epidermis and forms a mycelium within the tissue of the leaf. 11, A barberry leaf (lower surface), showing a group of aecidia (cluster cups). 12, Section of an aecidium on lower surface of barberry leaf. This is filled with chains of yellowish one-celled spores (aecidiospores). 13, A single aecidiospore. 14, An aecidiospore germinating on the surface of wheat, the germ tube penetrating a stoma. The parasite spreads within the tissue of the host and after a time uredospores are produced in characteristic pustules or sori as shown in (1). (Adapted from figure in a Bulletin of the Minnesota Experiment Station.)

5. *Aecidiospores*—in cluster cups or aecidia on the lower surface of barberry leaf.

Heteroecism.—Parasitic fungi, which like *Puccinia graminis*, have two different host species and can not carry through their complete life cycle unless both hosts are present, are called **heteroecious fungi.** By far the majority of parasitic fungi, however, require but a single host in

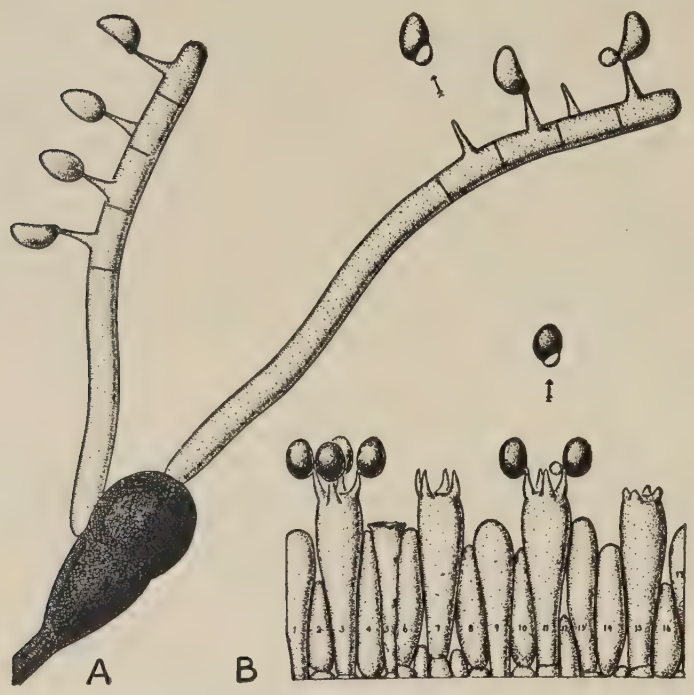


FIG. 301.—Spore-discharge in the Uredineae and the Hymenomycetes. *A*, a germinated teleutospore of *Puccinia graminis* (from *Avena sativa*) bearing two basidia, one with four ripe spores and the other with spore-discharge going on. *B*, a transverse section through the hymenium of *Psalliota campestris*, showing a basidium with four ripe spores and another basidium with spore-discharge going on. In both *Puccinia graminis* and *Psalliota campestris* a drop of water is excreted from the hilum of each spore just before discharge. Magnification the same both *A* and *B*, 880. (From Buller's *Researches on Fungi.*)

order to complete their life cycle. These are **autoecious.** A familiar autoecious rust is *Puccinia asparagi*, the asparagus rust.

Prior to 1865 the true relationship of the red rust stage, black rust stage, and barberry rust stage of *Puccinia graminis* was unknown. In fact, these three rusts were regarded as different species and

given different generic names, *Uredo*, *Puccinia*, and *Aecidium*, respectively.

The establishment of the fact that these were three different stages in the life history of a single organism is credited to the classical researches of the great German botanist, Anton de Bary.

For a number of years, the great importance of the barberry in spreading rust has been recognized. Denmark, in 1903, passed a barberry eradication law and since then almost all bushes have been eradicated from the country. This resulted in almost total elimination of black stem rust in Denmark. In 1918, a vigorous barberry

FIG. 302.—Leaf of common barberry (*Berberis vulgaris*), showing clusters of aecidia on the lower surface. (From Buller's *Researches on Fungi*.)

eradication campaign was initiated in this country by the Office of Cereal Investigations, of the United States Department of Agriculture, coöperating with the thirteen principal wheatgrowing states. Already, eradication has progressed so far in certain sections that the beneficial results are noticeable. It is not to be expected that destruction of all plants of those species of barberry which are subject to the disease will eradicate the disease in all localities. In regions where the winters are mild, uredospores may survive the winter and infect cereals in the spring, thus continuing the disease without the alternate host.

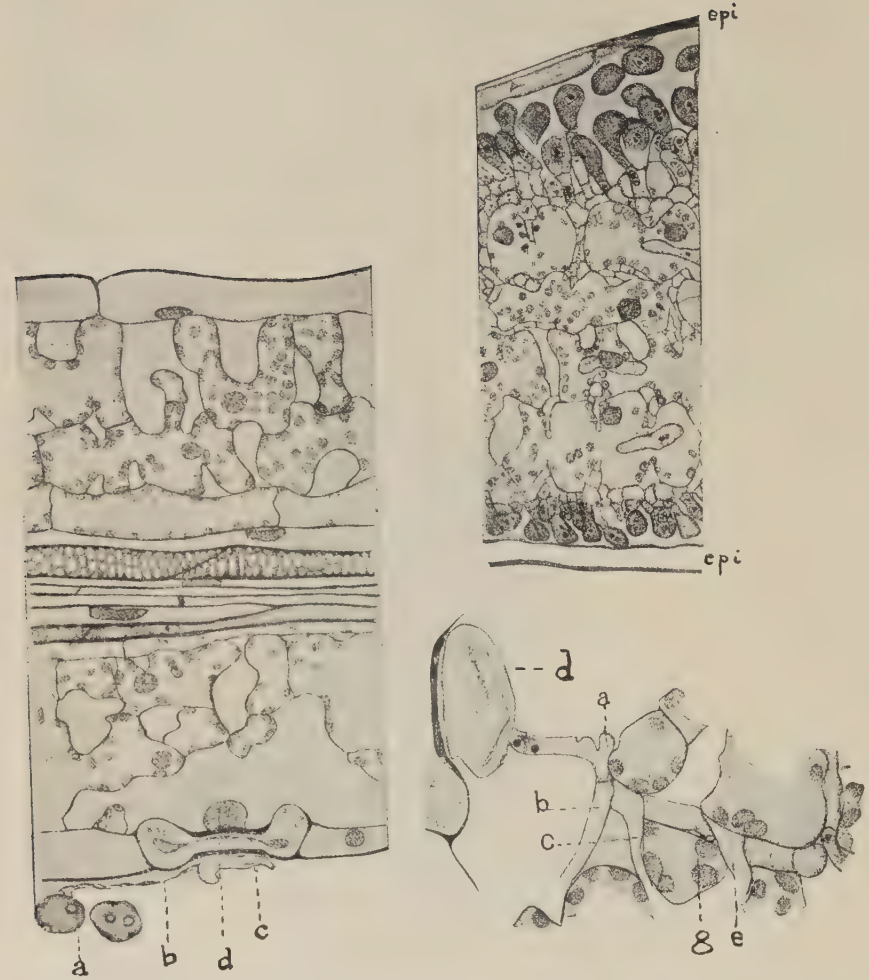


FIG. 303.—Infection of wheat by the leaf rust fungus, *Puccinia triticina*. The drawing to the left shows a section through a leaf of the host with two uredospores on the lower epidermis. One of the spores (*a*) has germinated and given rise to a germ tube (*b*) which is enlarged just outside the stoma (*c*) and just inside the stoma (*d*).

The lower right-hand drawing shows a portion of a section of a wheat leaf six days after infection by the rust parasite. *a*, *b*, *c* and *e* indicate hyphæ of the parasite among the mesophyll cells of the host. The large oval structure (*d*) is the expansion of the germ tube just inside the stoma (the same structure that is labelled *d* in the preceding drawing). The space containing the letters *a*, *b*, and *c*, is the air chamber beneath the stoma.

The upper right-hand figure shows part of a cross section of a wheat leaf nine days after infection had taken place. Just underneath the upper and lower epidermis (*epi*) uredospore sori are developing and among the mesophyll cells of the host fragments of fungus hyphæ are shown. (After Ruth Allen, in *Journal of Agricultural Research*.)

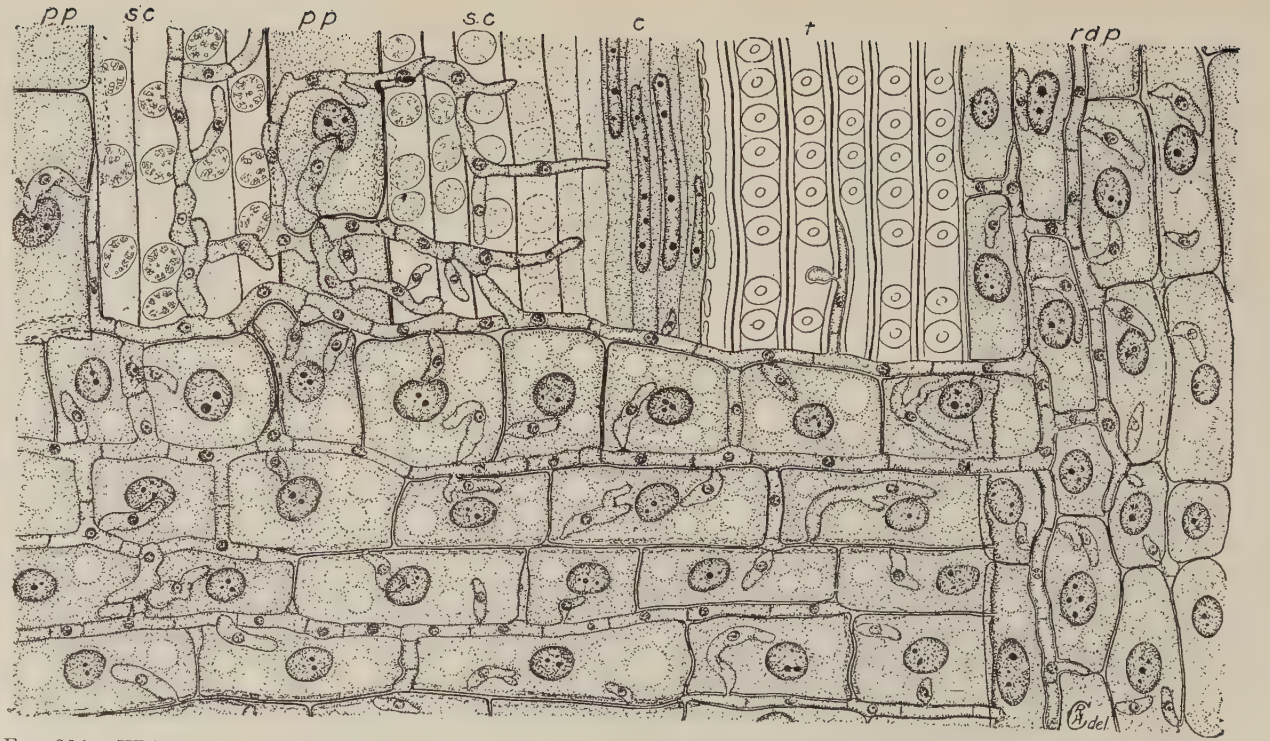


FIG. 304.—White pine blister rust, showing the relation of the mycelium of the rust, *Cronartium ribicola*, to the cells of the host (*Pinus strobus*). *pp*, phloem parenchyma; *sc*, sieve tubes; *c*, cambium cells; *t*, tracheids; *rdp*, resin-duct parenchyma. Note the number of haustoria which are shown entering the cells of the host. (After Colley, in *Journal of Agricultural Research*.)

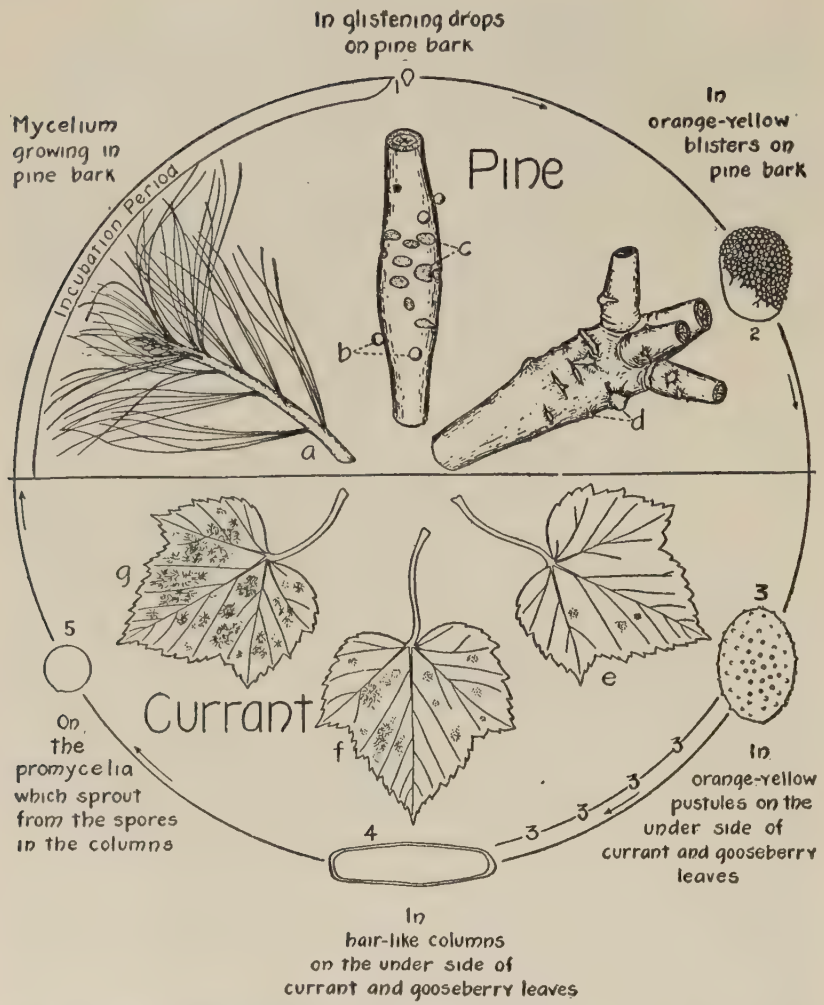


FIG. 305.—White pine blister rust. Diagram of the life cycle of the heteroecious rust, *Cronartium ribicola*. This rust has the spermagonial and aecidial stages on certain white pines chiefly (*Pinus strobus*), and the uredospore and teleutospore stages on currants (*Ribes* species). 1, spermatia; 2, aecidiospore; 3, uredospore; 4, teleutospore; 5, sporidium. *a*, a young pine branch at the time infection usually takes place; *b*, a drop of sugary fluid containing spermatia; *c*, spermagonia; *d*, aecidia; *e*, the dots on the currant leaf represent uredosori; *f*, the dots represent uredosori and the dashes teleutosori; *g*, condition of affected leaf in the fall when the teleutosori are predominant. (After Colley, in *Journal of Agricultural Research*.)

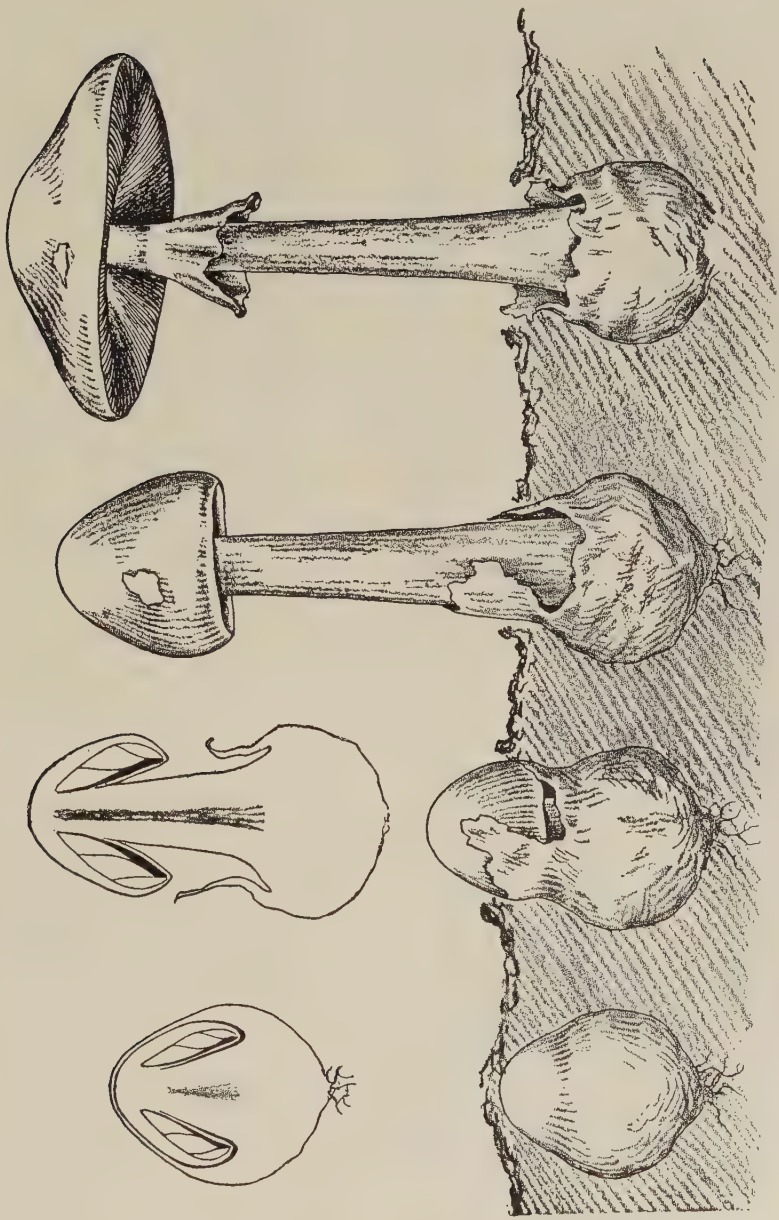


FIG. 306.—Stages in the development of a gill fungus (*Amanita*). See explanation in text. (After Longyear.)

EUBASIDIOMYCETES (FLESHY AND WOODY FUNGI)

This group includes the most familiar representatives of the Basidiomycetes, such as the mushrooms, puff-balls, and many other fleshy and woody forms. A characteristic feature of the group is the conspicuous sporophore which in some cases may attain considerable size and which produces the hymenium, a compact layer consisting of one-celled basidia, each bearing four basidiospores.

The Eubasidiomycetes consist of two sub-groups:

1. Hymenomycetes — in which the hymenium is exposed.

2. Gasteromycetes — in which the hymenium is enclosed.

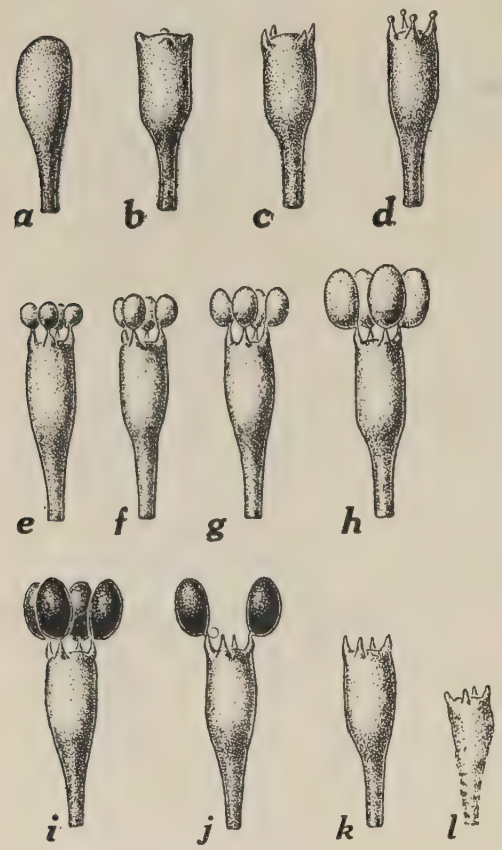


FIG. 307.—*Coprinus sterquilinus.* Stages in the development of a basidium and basidiospores, showing formation of basidium (*a–c*), development of spores (*d–i*), spore discharge (*j*), and degeneration of basidium (*k–l*). All of these stages are passed through in less than thirty-six hours. Magnification, 408×. (From Buller's *Researches on Fungi.*)

HYMENOMYCETES

The principal order of the Hymenomycetes is the *Agaricales.* This includes the gill fungi, the tooth fungi and the spore fungi.

A Common Gill Fungus.—Of all Eubasidiomycetes the gill fungi are the best known. The most familiar gill fungus is the cultivated mushroom (*Agaricus campestris*). The mushroom as we ordinarily know it is not the whole plant but merely a reproductive structure or sporophore. The vegetative part of the plant body is the mycelium which grows saprophytically in the soil or other substratum upon which the sporophores are produced. It consists of extensively branched strands of hyphae which absorb

and use as food, organic material in the sub-stratum. On this account mushrooms are never found except in locations where there is an abundance of organic material, such as decayed leaves and twigs, or manure. It is only after the mycelium has accumulated considerable stores of food that the sporophores are produced.

The mature sporophore, or fruiting body, consists of a stalk or stipe and an umbrella-shaped cap called the **pileus.** On the under side of this cap there are borne thin plates called **gills** which radiate from the stalk toward the margin of the pileus. The whole surface of the gills is covered with a layer made up of millions of basidia and sterile hyphae or paraphyses, all of which grow out at right angles to the surface of the hymenium.

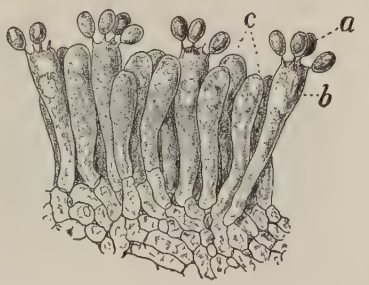


FIG. 308.—Small portion of a section through the spore-bearing layer (hymenium) of a mushroom. *a*, basidiospores; *b*, a basidium; *c*, paraphyses. (After Longyear, in Colorado Agricultural Experiment Station Bulletin.)

Mushroom "spawn," as sold by seedsmen, usually consists of dried manure and decaying leaves containing the mycelium of mushrooms which have previously grown upon this material. When a mushroom bed is being made this material is broken up, mixed with earth, and used to start the beds. The partially dried mycelium in the spawn grows rapidly in the moist warm substratum of the mushroom bed. The sporophores originate from strands of the subterranean mycelium. The first evidence of these is in the form of small rounded masses of interwoven hyphae known as " buttons," which are usually formed just beneath the soil surface. The stipe elongates, the cap expands, and the " mushroom " (sporophore) quickly assumes its typical shape. In the young sporophore there is a thin layer of hyphae which extends from the margin of the cap to the stipe, covering the gills. As development proceeds this layer is torn, but remnants of it may cling to the stipe, forming a "ring." The presence of a " ring " on the stipe is characteristic of the common edible *Agaricus*, as well as a number of other gill fungi. The young cap is often covered with a membrane, which is ruptured by the expanding cap and stipe, and remains at the base of the stipe as a cup or **volva.**

Basidiospores are produced in immense numbers on the hymenium. It has been computed that a single sporophore of *Agaricus campestris*, measuring 8 cm. in diameter, may liberate as many as 1,800,000,000 spores and a single fruiting body of *Polyporus squamosus* as many as

Fig. 309.—Semi-diagrammatic drawing of a section in a field illustrating the manner in which the spores of the Horse Mushroom (*Psalliota arvensis*) are liberated and dispersed. A slight lateral movement of the air is supposed to be carrying the spore-cloud away from the underside of the pileus. Reduced to $\frac{1}{2}$. (From Buller's *Researches on Fungi.*)

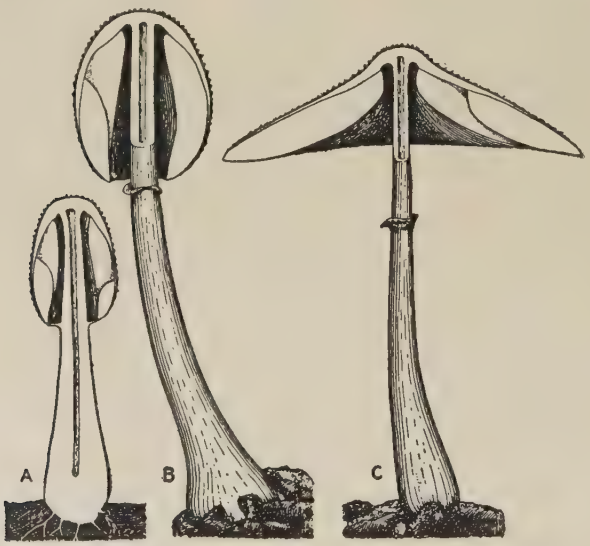


Fig. 310.—*Lepiota cepasestipes.* Sections of three fruit-bodies coming up among cinders, Sphagnum, etc., in a hothouse. *A*, in the morning, the gill-chamber still intact. *B*, in the afternoon, the pileus beginning to expand, an annulus left upon the stipe. *C*, at night, the pileus fully expanded and shedding spores. Natural size. (From Buller's *Researches on Fungi.*)

11,000,000,000. In the latter case the spores are liberated at an average rate of at least one million a minute. The spores drop from the sterigmata of the basidia upon which they are borne, and are readily carried far and wide by air currents. Under favorable conditions they germinate and develop a new mycelium, but it has been estimated that in the common mushroom, *Agaricus campestris*, only one spore in twenty billion actually germinates and grows into a mushroom plant.

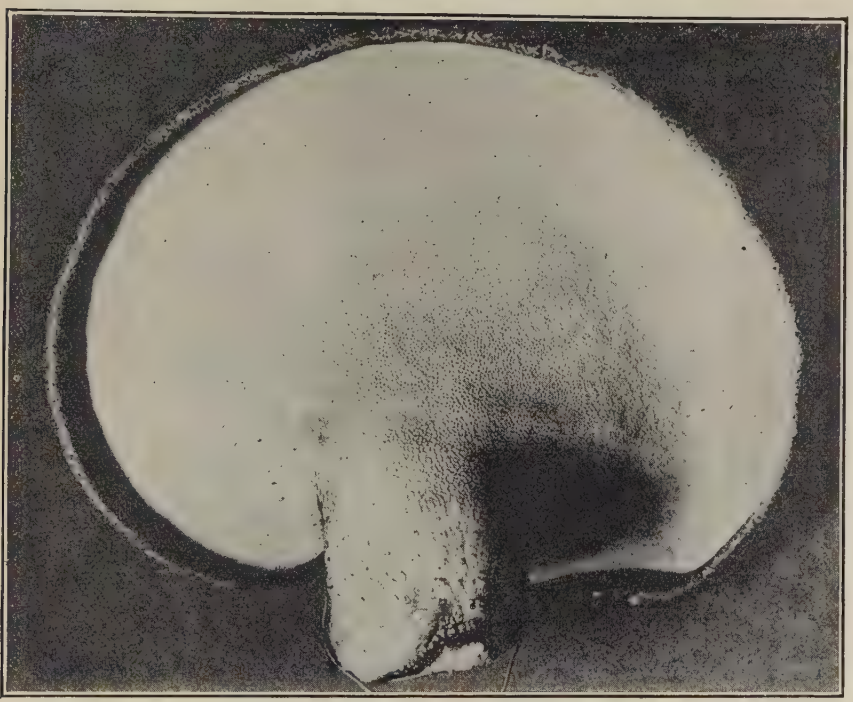


FIG. 311.—Under surface of fruit-body of *Polyporus squamosus* nearly full grown, showing the pores of the hymenial tubes and the reticulations on the stipe. The fruit-body was photographed immediately after it was cut; the involution of the edge of the pileus is quite natural. Photographed by R. H. Pickard. One-third natural size. (From Buller's *Researches on Fungi*.)

Kinds of Gill Fungi.—The gill fungi are divided into five groups, based upon the color of the spores, as follows:

1. White-spored.
2. Rose-spored.
3. Ocher-spored.
4. Purple-brown-spored.
5. Black-spored.

Spore color is readily determined by making a spore print. This

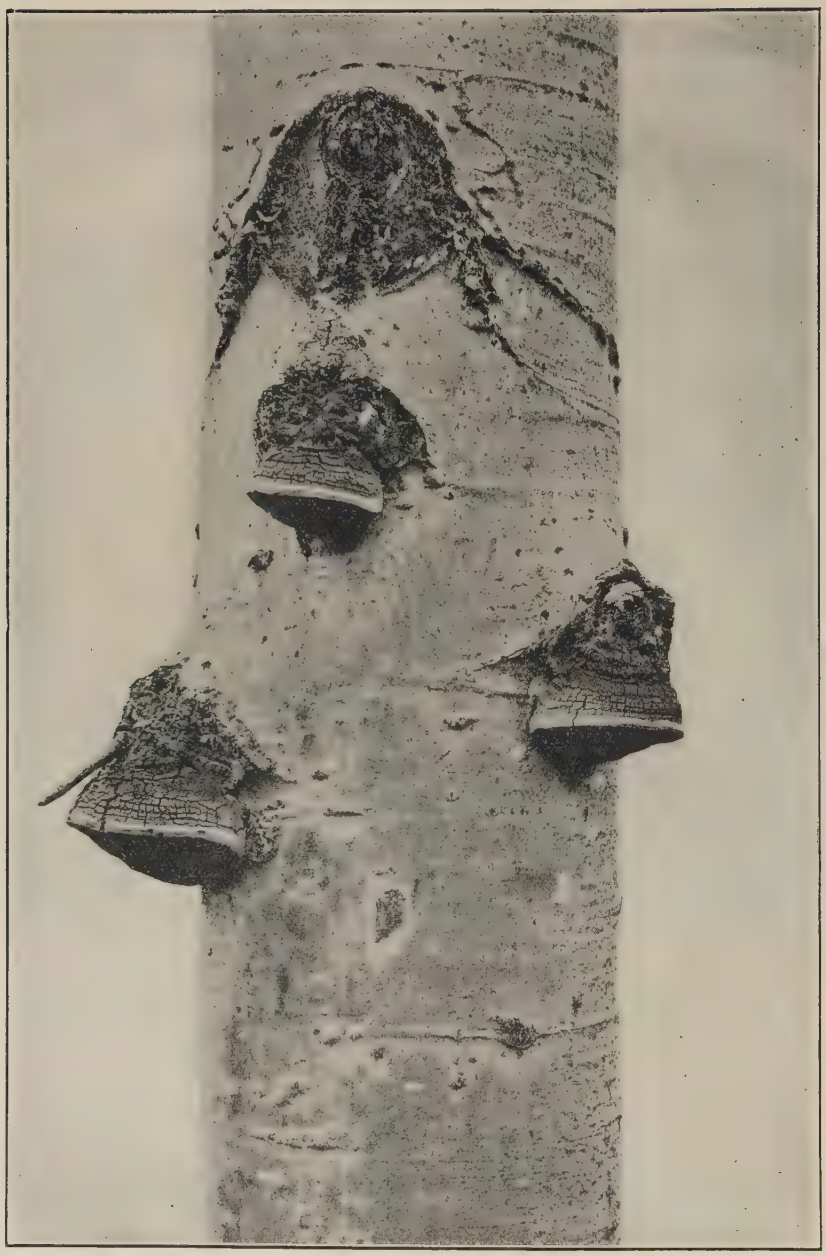


FIG. 312.—A living aspen trunk with several sporophores of the bracket fungus, *Fomes ignarius*. The vegetative mycelium is within the tissues of the stem. (After Von Schrenk and Spaulding, in *Journal of Agricultural Research*.)

is made by cutting off the cap, laying it with gills down on a piece of smooth paper, and covering to prevent spores from being blown away. Within twenty-four hours or less, spores will have been discharged in sufficient numbers to leave an imprint or copy of the gill arrangement and to determine their color.

White-spored gill fungi include the well-known genus *Amanita*, in which are found practically all the deadly poisonous species of gill fungi.

FIG. 313.—A cluster of puff-balls (*Lycoperdon*) (After Longyear.)

Amanita is distinguished by the following combination of characters:

1. White spores.
2. " Ring " on the stipe or stem.
3. Volva, or cup, at the base.

There are a number of species of *Amanita*, varying considerably in color, size, and other minor features, but all of them have the characteristics given above. Some *Amanita* species are not only not poisonous but are in fact edible.

The common or cultivated mushroom (*Agaricus campestris*) is a purple-spored form, with pink gills, a broad " ring " on the stipe, but no volva. The black-spored gill fungi include the well known " inky cap " and " shaggy mane " (*Coprinus* species). In these, the gills finally dissolve, forming a black inky liquid.

Tooth Fungi.—The members of this group have sporophores which are distinguished by the presence of teeth or spines which bear the hymenium. It includes both fleshy and leathery forms. *Hydnum* is the best known genus in the family, several species of which cause wood rots.

Pore Fungi.—In this group, the spores are borne in open tubes or pits. Certain species of pore fungi are among the most destructive wood-rotting fungi. The fruiting body is frequently woody, leathery, or corky in texture. It is often shelf-like or bracket-like in shape, and may grow to a large size. The sporophores of pore fungi are often found on trees.

GASTEROMYCETES—PUFF-BALLS

This assemblage of fleshy fungi has the hymenium enclosed within a covering known as the **peridium.** The puff-balls (Lycoperdales) are the best-known representatives. In some genera, the peridium consists of a single layer, whereas in others it has two layers. For example, in the earth-star (*Geaster*) the outer peridial layer splits open, when the spores are mature, into star-like lobes, and later those lobes become reflexed, whereas the inner layer opens by a terminal pore. The inside of a young, immature puff-ball consists of a white, fleshy tissue, which becomes chambered as development proceeds. In some genera, these chambers are filled with interwoven hyphae, the lateral branches of which end in basidia, whereas in other genera the walls are lined with basidia.

Other quite common representatives of the Gasteromycetes are the bird's nest fungi (Nidulariaceae) and the stink horns (Phallaceae).

BASIDIOMYCETES—A SUMMARY

1. This group includes both parasitic and saprophytic fungi. Many cause destructive plant diseases.
2. The hyphae are septate and branched.
3. No motile spores are produced.
4. The characteristic feature of the class is the occurrence in the life cycle of a basidium, which produces asexual spores.
5. Gametangia have not been found. There are simple nuclear fusions, however, which serve as fertilization processes.
6. The Basidiomycetes are considered to be the highest of the fungi, and to have been derived from the Ascomycetes. The basidium has a place in the life history similar to that of the ascus.

CHAPTER XIII

THE BRYOPHYTA (LIVERWORTS AND MOSSES)

CHARACTERISTICS OF THE DIVISION

As pointed out in Chapter XI, the algae, with few exceptions, are aquatic plants. By far the majority of them live submerged in fresh or salt water. Practically all the others are found on wet substrata or at least carry on an active existence only during periods when moisture is abundant. The Bryophyta, on the other hand, are truly terrestrial or land plants, although their adaptation to land conditions is so imperfect that few of them, if any, are able to complete their life cycle without being subjected to a period during which the plant is covered with water. They are also unable to vegetate actively during very dry periods, because of their relatively inefficient water absorbing and conserving tissues.

Another very important characteristic of the Bryophyta is the fact that in all of them there is a distinct alternation of generations. It was stated in the chapter on the algae that in all plants having sexual reproduction the zygote nucleus has twice as many chromosomes as the nuclei of the gametes, and that somewhere in the life cycle of all such plants there is a reduction division by which the double (diploid) chromosome number is reduced to the haploid number characteristic of the gametes. In the simpler algae having sexual reproduction, this reduction division takes place at the time of germination of the zygospore or oospore. Accordingly, "the plant" has nuclei with the haploid chromosome number.

It will be recalled that in a number of the Rhodophyceae the reduction division is delayed for a long time. For example, in the life cycle of *Polysiphonia* and many other red algae, there are two different plants which alternate with each other. These are (1) the asexual plant which has the diploid chromosome number and which produces tetraspores with the haploid chromosome number, and (2) the sexual plant arising from a tetraspore and having the haploid chromosome number. These sexual plants produce the gametes whose fusion again doubles the number of chromosomes. This alternation of diploid and haploid

plants, which is generally spoken of as **alternation of generations,** occurs also in some Phaeophyceae but it is by no means characteristic of the Thallophyta as a whole. It is, however, characteristic of the Bryophyta and of all the Pteridophyta and Spermatophyta.

The terrestrial habit and the constant occurrence of alternation of generations in the life cycle are the two most significant characteristics distinguishing the Bryophyta from most Thallophyta. They are briefly restated in the following summary of the characteristics of the Bryophyta:

1. With the exception of a few forms the Bryophyta are terrestrial or epiphytic. The liverworts and mosses in general show marked preference for moist habitats. Those which grow in dry places often show a remarkable power to survive extreme desiccation, but they carry on their growth and other life processes actively only during wet or very moist periods.

2. Alternation of generations takes place in all the members of this division.

3. The asexual plant (**sporophyte**) is smaller than the sexual plant (**gametophyte**). It is permanently attached to and grows more or less parasitically upon the gametophyte, never establishing direct connection with the soil.

4. The epidermal cells are provided with a cuticle, which is lacking in the case of the Thallophytes.

5. No true roots are formed in this division, but the sexual or gametophyte plants produce organs called **rhizoids**, which perform the functions carried on by the roots of ferns and seed-bearing plants.

6. Sexual reproduction is heterogamous, as in all plants above the Thallophytes. The female gametangium (called the **archegonium** in the Bryophyta and Pteridophyta) does not consist of a single cell, the protoplasm of which forms one or several female gametes (egg cells) as does the oogonium of the Thallophyta. Instead it is a **multicellular** flask-shaped **organ,** and the single egg cell is surrounded by a wall made up of **many cells,** instead of being surrounded by a **cell wall only** as in the Thallophytes.

7. The antheridia of the Bryophyta are also distinctly different from those of the Thallophyta, the wall surrounding the sperms produced by one antheridium being made up of a **layer of cells** instead of consisting, as in the Thallophyta, merely **of a cell wall.** This applies as well to the Pteridophyta as to the Bryophyta.

8. Fertilization can not take place unless the plants are wet, for it must be possible for the sperms to swim to the archegonia.

9. The asexual spores of the Bryophyta (and the Pteridophyta and

Spermatophyta as well) are formed in groups of four (**tetrads**) each tetrad being formed as the result of two divisions of a single cell (the spore mother cell).

The Bryophyta are divided into two classes, the Hepaticae or liverworts and the Musci or mosses.

THE HEPATICAE. (LIVERWORTS)

The members of this class are in general more strictly confined to very moist habitats than are the Musci. There are some species, however, notably certain forms growing in California and in other regions where there is a long dry season, which are able to survive months of almost complete desiccation. The sporophytes of the liverworts are less complex than are those of the mosses and for the most part somewhat smaller.

We shall describe the structure, development, and reproduction of two representatives of the Hepaticae and call attention to the principal variations from these types.

RICCIA

This and the closely related genus *Ricciocarpus* have the simplest sporophytes (asexual phase) of all liverworts, although their gametophytes are not so simple as are those of certain other members of the class. *Riccia fluitans* is a species which frequently grows submerged in water but which never forms gametangia or gives rise to sporophytes when growing immersed. *Ricciocarpus natans* is generally found floating on the surface of water. Both of these species, however, can grow upon moist soil when the water dries up or recedes.

FIG. 314.—Thallus of a terrestrial species of *Riccia*. (Magnification about 12×.)

The Gametophyte.—The gametophyte of the land-living species of *Riccia* is a small, flattened, dorsiventral thallus which branches freely by dichotomy (forking) and thus frequently takes on a rosette form (Fig. 314). *Riccia* plants can often be found on bare moist ground in early spring. The middle line of the thallus is thickened and forms a sort of midrib, and there is a long depression on the upper side of the thallus and along the middle line. From the under side of the thallus numerous rhizoids grow out. These are very similar to root

hairs and are merely tubular extensions of certain of the cells of the lower surface of the thallus. They function as organs of attachment and water absorption. In addition to the rhizoids there are also borne on the under side of the thallus a series of broad overlapping scales. At the end of each branch of the thallus and at the bottom of the median furrow there is a single cell called the **apical cell,** which by its repeated division gives rise to daughter cells from which are formed all the new tissue of the growing branch. Thus the gametophyte grows at the tip as do the stems and roots of the higher plants, but the "primordial meristem" consists of a single cell instead of a group of cells as in the higher plants. If a cross section of the thallus (Fig. 315) be examined it is found that the upper or dorsal portion is made up of cells containing chloroplasts, while the lower or ventral part consists of colorless cells. There are many clefts extending from the upper surface of the thallus down into the chlorophyll-bearing tissue. These function, like the stomata and intercellular spaces of leaves, in giving access of air to the cells which carry on photosynthesis. The colorless cells below the green layer serve for water and food storage.

FIG. 315.—Cross section, somewhat diagrammatic, of the thallus (gametophyte) of *Riccia* showing on the left an unfertilized archegonium sunk in a deep depression. On the right is a sporophyte within the enlarged venter of an archegonium from the fertilized egg cell of which the sporophyte developed. The chlorophyll-bearing tissue of the upper portion of the thallus is also shown as well as the colorless tissue of the lower part of the thallus, and the rhizoids. (Magnification about 30×.)

The Gametangia.—Each antheridium and archegonium is sunk in a deep depression in the thallus, opening out into the median furrow. Antheridia and archegonia are found on the same gametophyte thallus; that is to say, the species of *Riccia* are **monoecious.** In many species of liverworts, mosses, and ferns, antheridia and archegonia are never produced on the same gametophyte. Such species are said to be **dioecious.**

In *Riccia,* antheridia and archegonia in various stages of development may be found on a single plant, those nearest to the ends of the branches being in earlier stages of development than those farther back.

Antheridia.—These are more or less pear-shaped organs with a short stalk at the broader end. There is a single layer of sterile cells which forms the wall of the antheridium and encloses, in antheridia which are almost mature, several hundred cells with relatively large nuclei and

dense cytoplasm. These latter are the sperm mother cells, each of which, by a single nuclear division and a subsequent oblique division of the cell cavity, gives rise to two sperm cells. The protoplast of each sperm cell forms a single biciliate sperm.

Archegonia.—The female gametangia in *Riccia* are in no important particular different from those of other genera of the Hepaticae, and so may be taken as typical of the whole group. Each mature archegonium consists of an enlarged basal portion, the **venter,** and a slender and elongated tubular portion called the **neck.** The base of the venter is attached to the tissue at the bottom of the depression in which each archegonium is enclosed. The neck reaches almost or quite to the top of the depression where it opens into the median furrow of the thallus. Within the single layer of cells which forms the wall of the venter and neck is a single row of cells. The largest of these cells occupies most of the cavity of the venter. It has a large nucleus and dense cytoplasm and is the female gamete. The cell just above it is the **ventral canal cell.** Though the ventral canal cell and the egg cells have been formed by the division of a single cell, the ventral canal cell never functions as a gamete. The other cells of the axial row are called the **neck canal cells.** They are four in number in *Riccia* but more numerous in some other liverworts. The walls separating the neck canal cells from each other generally break down before the archegonium is mature, and the protoplasts of the neck canal cells and ventral canal cells degenerate into a mucilaginous mass.

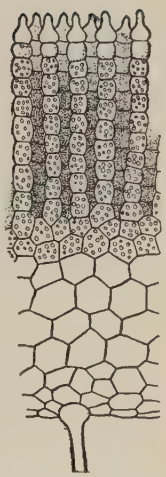


FIG. 316.—A portion of a cross section of the thallus of a species of *Riccia* showing the chlorophyll-containing tissue, the colorless region, and the origin of a rhizoid. Magnification about 100×. (Redrawn after Casares-Gil.)

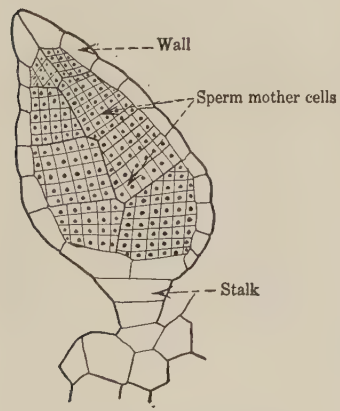


FIG. 317.—An antheridium of *Riccia* in section.

Fertilization.—The union of the male and female gametes can not take place in *Riccia,* nor in fact in any of the liverworts, mosses, or ferns, unless the gametophyte plants are wet. Even though fully developed, the archegonia and antheridia do not open except after the plants have been wet by rain or heavy dew. Furthermore, even if freed from the

antheridia, the sperms can reach the archegonia only by swimming in water. When gametophytes bearing mature archegonia are wet, water is absorbed by the mucilaginous remains of the ventral canal and neck canal cells, and as the result of the swelling of this mass the **cover cells,** closing the neck canal, are forced apart. The mucilage is soon dissolved away so that there is an open passage down the neck canal to the cavity of the venter, where the egg, a spherical, naked protoplast, awaits fertilization. At the tip of the antheridium some of the sterile cells forming the wall of the antheridium are forced apart as the result

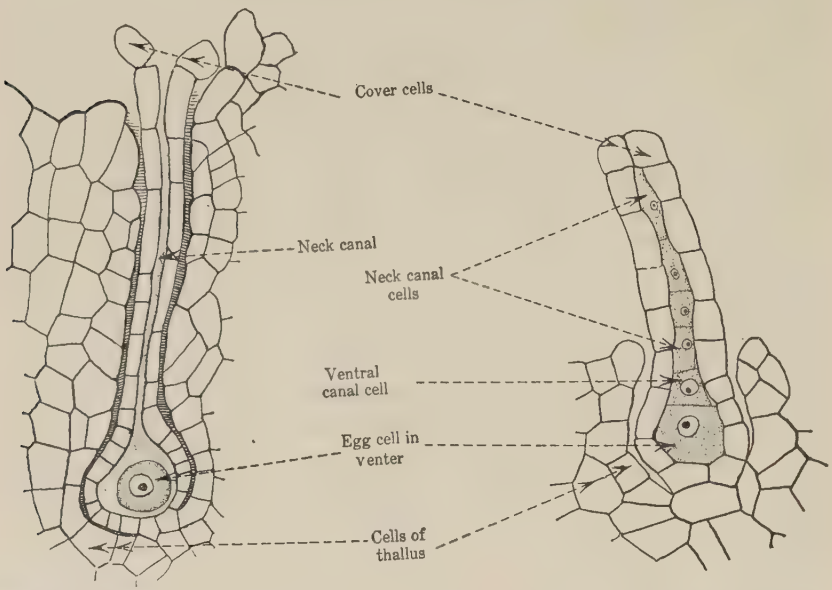


FIG. 318.—Archegonia of *Riccia* surrounded by the tissue of the thallus. To the right, an almost mature archegonium. To the left, an archegonium ready for fertilization. (Drawn from preparations of D. H. Campbell.)

of the swelling of the disorganized walls of the sperm mother cells. Thus the sperms escape. Each sperm is a small spirally twisted structure made up mostly of nuclear material but including also some cytoplasm. The two cilia are several times as long as the body of the sperm.

The sperms have a tendency to move towards certain of the substances discharged from the archegonium neck (a phenomenon known as **positive chemotaxis**), and so in their swimming they are directed toward the archegonia. On this account and because hundreds of sperms are produced to one archegonium, few egg cells fail of being fer-

tilized. Though a number of sperms may find their way into a single archegonium only one enters the egg and fertilizes it. Almost immediately upon the entrance of the sperm into the egg, a thin cellulose wall is formed about the resulting zygote. The nuclear material, which makes up practically the entire sperm, fuses with the nucleus of the egg, the resulting zygote nucleus having therefore twice the chromosome number characteristic of the gametophyte and gametes. The formation of the zygote by fertilization marks the beginning of the sporophyte or asexual generation.

The Sporophyte.—The zygote now increases in size until it almost fills the venter of the archegonium and then by division becomes a two-

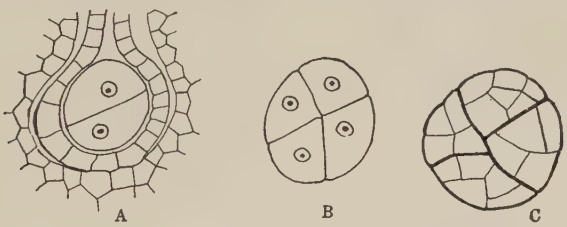


Fig. 319.—Successive early stages in the development of the sporophyte of *Riccia*.

celled **embryo.** By repeated cell divisions the embryo sporophyte grows into a spherical mass of cells many times the size of the zygote. Meanwhile the venter of the archegonium keeps pace with the embryo in its growth. The sporophyte, even after it has reached maturity, and the enlarged archegonium venter remain within the tissue of the gametophyte thallus. A short time before the sporophyte reaches maturity it consists of a wall made up of a single layer of flattened sterile cells and within this wall a number of free spherical cells with dense cytoplasm and large nuclei. Each of these cells, which we shall call spore mother cells, gives rise to a tetrad or group of four spores.

Spore Formation.—Up to this point all the cells of the sporophyte have the diploid chromosome number, but the first of the two nuclear divisions by which each spore mother cell produces four spores is a reduction division by which the chromosome number is reduced to the haploid number. The nuclei resulting from this reduction division may be spoken of as the **spore mother nuclei.** They almost immediately undergo a second division which is, however, not a reduction division but an ordinary mitosis, so that the four spore nuclei have the haploid chromosome number. Each of these nuclei, together with some cytoplasm and considerable stored food, becomes surrounded by a thin wall which thickens as the spore ripens. By the time the spores

have fully matured the single layer of cells forming the walls of the sporophyte and the cells of the enlarged archegonium venter have broken down.

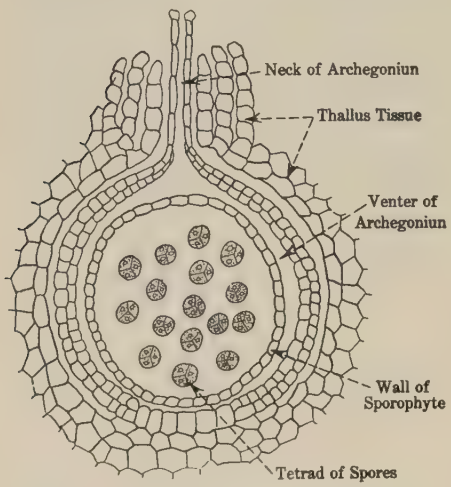


FIG. 320.—Diagrammatic figure showing in cross section, the mature sporophyte, enlarged archegonium, and thallus of *Riccia*.

Germination of Spores.—The spores are freed by the decay or shriveling of the gametophyte and under favorable conditions germinate to form new gametophyte plants. The coat of the mature spore consists of two layers, the **exine,** which is relatively thick and dark in color, and a thin and more delicate inner layer called the **intine.** At germination the protoplast of the spore absorbs a considerable quantity of water and swells. As a result the exine is ruptured and the intine is stretched so that it protrudes in the form of a short, blunt germination tube. This soon grows, no doubt largely because of continued water absorption and the resulting stretching of its wall, until it forms a tube of a length several times as great as the diameter of the spore. Most of the protoplasm of the spore, including oil drops and granules of other stored foods, passes out into the tube. Chloroplasts appear and increase in number, and soon the enlarged end of the germination tube is cut off by a transverse wall. By repeated division of the terminal cell a group of eight cells is formed. One of these cells becomes the apical cell. By successive divisions of this apical cell there are cut off cells from which all new tissue is derived. Thus a new gametophyte plant arises.

FIG. 321.—Two early stages in the development of the gametophyte of *Riccia* from the spore. None of the cell contents has been shown.

Life Cycle of Riccia.—By way of summary, we may state the principal stages in the life cycle of *Riccia* as follows (Fig. 322):

1. The gametophyte thallus which absorbs water and mineral

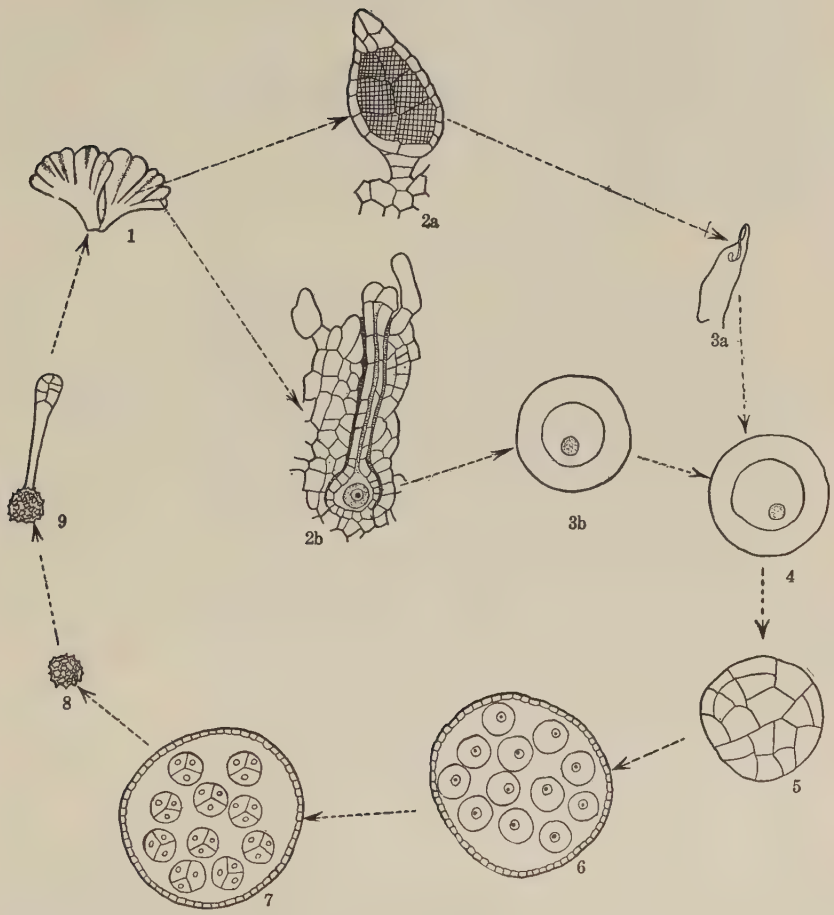


FIG. 322.—Diagram showing the life cycle of *Riccia*. 1, the gametophyte thallus (monoecious). 2*a*, an antheridium. 2*b*, an archegonium ready to open and permit the entrance of sperms (both antheridia and archegonia are sunk in the tissue of the thallus). 3*a*, a single sperm. 3*b*, an egg cell. 4, the fertilized egg cell or zygote. 5, an embryo sporophyte resulting from repeated divisions of the zygote. 6, the sporophyte with contained spore mother cells. 7, tetrads of spores each such group of four resulting from two divisions (the first a reduction division) of a spore mother cell. 8, a single ripe spore. 9, a very young gametophyte plant developed from a spore. Note that stages 4–6 and the wall cells in 7 belong to the sporophyte generation, the other structures to the gametophyte.

salts from the soil and carbon dioxide from the air and which carries on photosynthesis.

2. The development upon this thallus of the gametangia (antheridia and archegonia).

3. The formation within each antheridium of hundreds of sperms and within each archegonium of one egg cell.

4. The opening of the archegonia and antheridia after maturity and when the plants are wet.

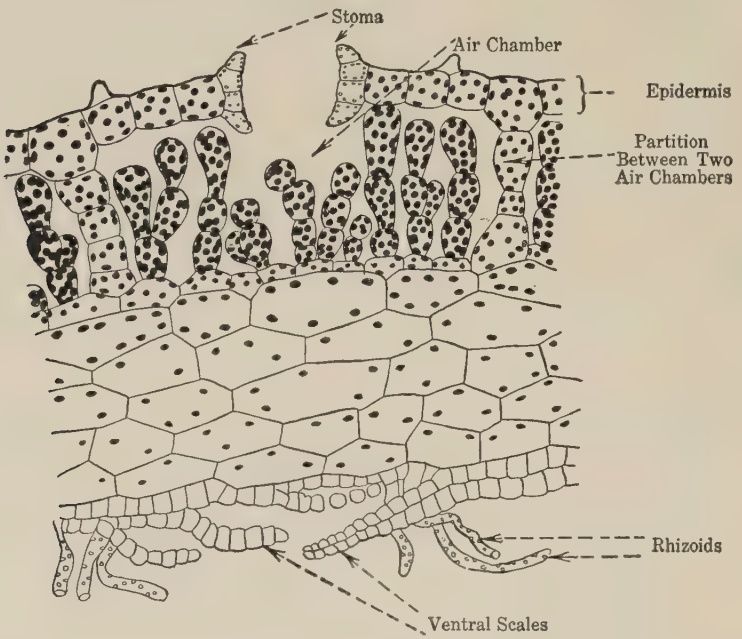


FIG. 323.—Cross section through a portion of the thallus (gametophyte) of *Marchantia*. Note in the air chambers the short, sometimes branched filaments of cells, provided with numerous and large chloroplasts.

5. Swimming of sperms to archegonia and fertilization of egg cell by a sperm.

6. The fusion cell (zygote) with its diploid nucleus formed by the fusion of the haploid nuclei of the two gametes.

7. Development from the zygote of a globular sporophyte consisting of a single outer layer of sterile cells enclosing a number of spore mother cells having the diploid chromosome number.

8. Reduction division of each mother nucleus to form two haploid nuclei.

9. Division of these by ordinary mitosis to form nuclei of a tetrad of spores.

10. Liberation and germination of the spores and development of a new gametophyte.

MARCHANTIA

We have chosen *Riccia* as the first bryophyte type for discussion because it has the simplest sporophyte of all living Bryophyta, although a number of liverworts have much simpler gametophytes. As a second type we shall consider the relatively common and widely distributed *Marchantia* which has a considerably more complex sporophyte than *Riccia*.

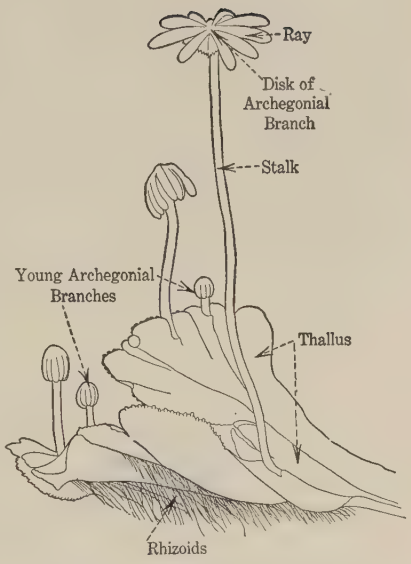


FIG. 324.—A portion of the female gametophyte of *Marchantia*.

The Gametophyte.—In *Marchantia* the gametophyte, like that of *Riccia*, is a dichotomously branched thallus bearing on the lower side rhizoids and thin scales. *Marchantia* is dioecious, for instead of archegonia and antheridia being borne on the same gametophyte, certain thalli bear archegonia and others antheridia (Figs. 324 and 325). Antheridia and archegonia are never both found on the same gametophyte. Moreover, the gametangia, instead of being borne buried in depressions in the thallus as in *Riccia*, are produced on special erect thallus branches. The arrangement of the cells which carry on photosynthesis is quite different in the gametophyte of *Marchantia* from that of

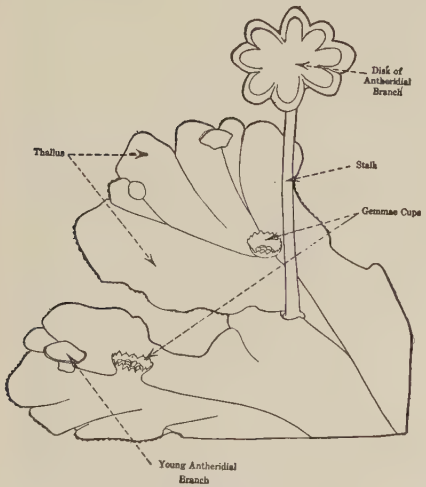


FIG. 325.—A portion of the male gametophyte of *Marchantia*, showing antheridial branches and gemmae cups. The latter are also sometimes produced on the female gametophyte.

Riccia. Just below the upper surface there are a large number of shallow air chambers. From the floor of each of these there arise short, sometimes branched filaments of cells which are provided with numerous and large chloroplasts and which are the principal carbohydrate-making cells. These chambers are completely roofed over by an epidermis except for a single pore which permits the ready entrance and exit of gases.

Reproduction by Gemmae.—*Marchantia* and a number of other related liverworts are capable of multiplying themselves even without the formation of gametangia. This is accomplished by means of out-

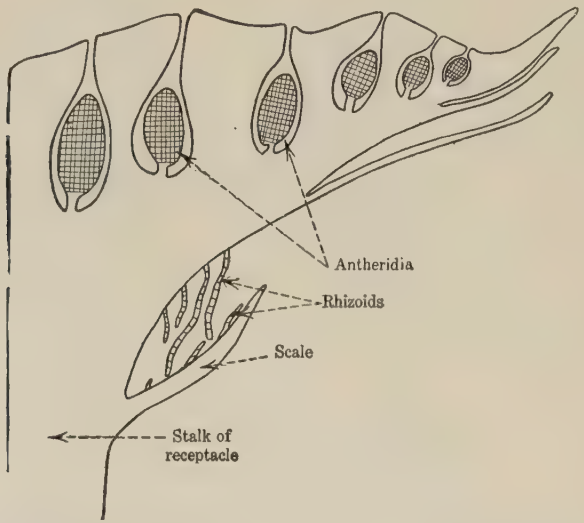


Fig. 326.—Diagram of half of an antheridial disk of *Marchantia*, showing the position of the antheridia. The antheridia are essentially the same in structure as those of *Riccia* as shown in Fig. 317 and have a wall one cell layer thick, not shown in this diagram, within which are great numbers of sperm-producing cells.

growths of the thallus specially adapted to vegetative reproduction (Fig. 325). They are called **gemmae.** When separated from the gametophyte they may grow into a new gametophyte thallus in a manner somewhat comparable to the growth of a rose or carnation plant from a small stem cutting. The gemmae are produced in structures called **gemmae cups** which are borne on the upper surface of the thallus.

Antheridia and Archegonia.—There is no essential difference in the structure of the gametangia in *Marchantia* and *Riccia.* The antheridial branch has a slender stalk surmounted by a disc with lobed edge. Numerous antheridia are produced on each antheridial branch, each antheridium being enclosed within a cavity in the disc. These cavities

open on the upper surface of the disc and it has been shown in the case of *Fimbriaria*, a genus closely related to *Marchantia*, that, at the time the ripe antheridia open, their contents may be projected several centimeters into the air. It is not unlikely that this may occur also in *Marchantia*. When thus launched into the air the male gametes are no doubt often carried some distance by air currents and thus the chances of their reaching an archegonial plant are somewhat increased.

The archegonial branch consists of a slender stalk surmounted by a small disc with a number of radiating and drooping rays. The archegonia are borne on the under side of the disc between the rays and hang downward. At the time when the archegonia are just mature the stalk of the archegonial branch is still only a few millimeters long, but it continues to lengthen even after the archegonia are fertilized.

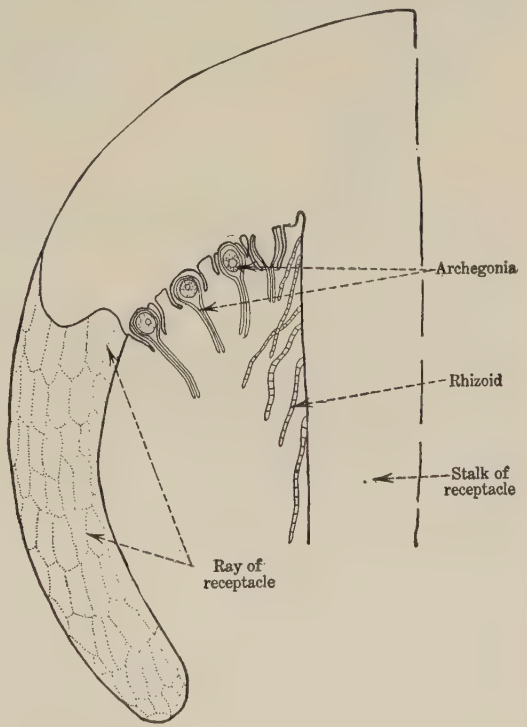


FIG. 327.—Diagram of half of an archegonial receptacle of *Marchantia*, showing the position of the archegonia.

The Sporophyte.—In *Marchantia* the process of fertilization and the early stages of the development of the embryo sporophyte from the zygote (fertilized egg cell) are very similar to those in *Riccia*. The mature sporophyte is, however, very different (Fig. 328). Instead of consisting merely of a sphere of cells of which all but a single outer layer become transformed into spores, the mature sporophyte is made up of three distinct parts (the **foot, seta,** and **capsule**) and many of its cells are sterile, that is, do not give rise to spores. The foot is an expanded basal portion which attaches the sporophyte to the gametophyte tissue on the under side of the archegonial disc. The capsule is similar in structure

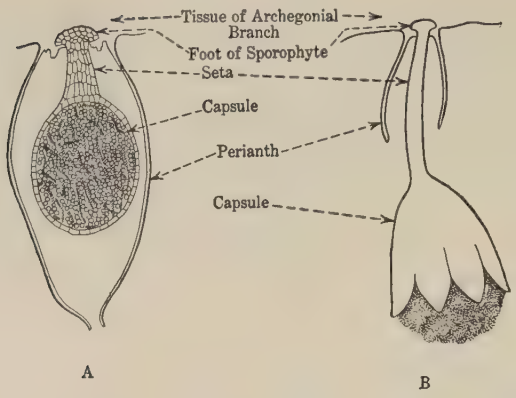


FIG. 328.—*Marchantia*. *A*, median longitudinal section of an immature sporophyte. *B*, mature sporophyte, with capsule dehiscing. In both figures, a portion of gametophytic tissue is shown.

to the whole sporophyte of *Riccia*, being oval in form and consisting of a single outer layer of sterile cells within which the spores are produced. By sterile cells is meant cells which are not directly concerned with reproduction. The seta is a short stalk which connects the foot and the capsule.

As the embryo sporophyte develops, the venter of the archegonium enlarges, keeping pace with the growth of the sporophyte and forming an envelope called the **calyptra.** This is not ruptured until just before the complete maturity of the sporophyte, when the seta elongates very rapidly. Meanwhile the foot of the sporophyte penetrates the tissue at the base of the archegonium and this tissue grows up around the foot. As a result the sporophyte becomes firmly attached to the gametophyte and is able to absorb the water and food which are necessary for its development. Not only are the cells forming the wall of the capsule, as well as all the cells of the seta and foot, sterile, but even within the capsule there are some sterile cells. These sterile cells which develop among the spores are the **elaters,** elongated spindle-shaped cells with spiral thickenings on the inner surface of the walls. The elaters are hydroscopic, and after the rupture of the capsule wall they bend and twist in response to changes in atmospheric humidity. These movements assist in the dissemination of the spores. The position of the sporophyte, hanging pendent from the under side of the rays of the archegonial branch, is also favorable to spore dissemination, for the stalk of the archegonial branch may be as long as 2 centi-

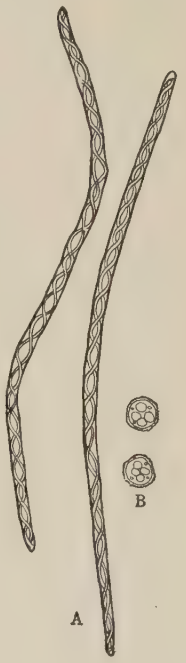


FIG. 329.—Elaters (*A*) and spores (*B*) of *Marchantia*.

meters at maturity. The spores falling from the open capsule are very likely to be carried away by air movements and thus distributed to some distance.

Germination of Spores and Development of the Gametophyte.—The development of spores from the spore mother cells in *Marchantia* does not differ in any important particular from the same process in *Riccia*. It should be borne in mind that in *Marchantia* as in *Riccia* all the stages in development from the formation of the zygote until the first division of the spore mother cells belong to the diploid or sporophyte

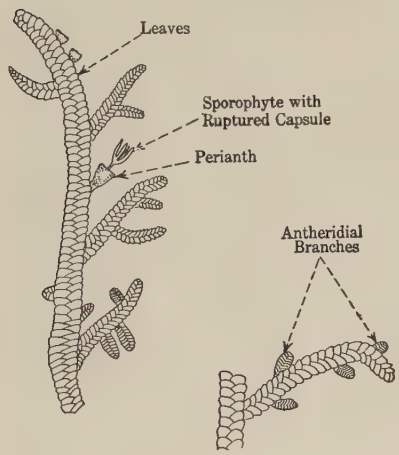


FIG. 330.—A leafy liverwort (*Porella*). At left, a portion of a female gametophyte; at right, a portion of a male gametophyte.

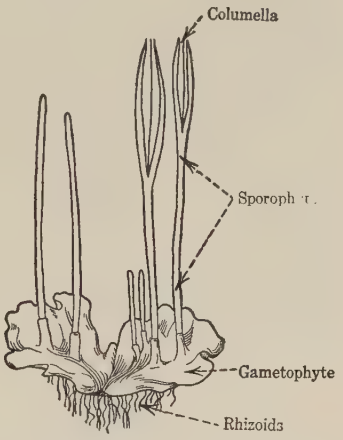


FIG. 331.—Plant of a species of *Anthoceros*, showing gametophyte thallus with attached sporophytes of which two (to the right) have split open at the ends.

phase or generation. The nuclei of the spores and also the nuclei of the cells resulting from the first division of spore mother cells have the haploid chromosome number and belong therefore to the gametophyte generation. Spore germination and the development of the gametophyte in *Marchantia* do not differ essentially from the corresponding processes in *Riccia*.

Comparison of Marchantia with Riccia.—The following are some of the most important points of difference between the two liverworts thus far discussed.

1. The gametophyte of *Marchantia* is considerably more differentiated than that of *Riccia*. This is particularly true as regards the epidermis, the food-making tissue, and the provision for aeration.

2. *Marchantia* is dioecious while *Riccia* is monoecious.

3. Antheridia and archegonia are borne on special branches of the gametophyte in *Marchantia*, but in *Riccia* are merely sunk in the tissue of the thallus proper.

4. The sporophyte of *Marchantia* is larger than that of *Riccia* and more complex. It consists of a foot which acts as an organ for attachment and absorption, a stalk or seta, and the capsule within which the spores are formed.

5. Much of the sporophyte of *Marchantia* is made up of sterile cells, i.e., there is relatively much less sporogenous tissue in the sporophyte of *Marchantia* than in *Riccia*. Even within the capsule, some of the cells instead of forming spores develop into peculiar sterile cells called elaters.

6. In *Marchantia* there is rather effective provision for the distribution of spores, whereas such provision is lacking in *Riccia*. In the former plant the fact that the sporophyte is not buried in the gametophyte tissue, its attachment in a pendent position to the under side of the stalked archegonial branch, the presence of a seta, and the presence of elaters among the spores all favor dissemination. In *Riccia*, on the other hand, the spores, buried within the gametophyte, escape only by the disintegration of the tissue of the latter.

OTHER LIVERWORTS

Both *Riccia* and *Marchantia* are thallose liverworts, but a very large number of the liverworts are leafy. In the leafy forms the gametophyte generally consists of a more or less prostrate dorsiventral stem bearing simple, generally close-set leaves and numerous rhizoids. Although there is greater differentiation externally, there is not so great a variety of tissues as in such thallose forms as *Riccia* and *Marchantia*, for the whole gametophyte is made up of very similar green parenchyma cells. The leaves are but a single layer of cells thick and have no midrib. The antheridia and archegonia, which are borne upon the leafy branches, are not essentially different from those of the forms already described. The sporophytes resemble those of *Marchantia*, although generally the stalk or seta is relatively longer. *Porella*, one of the commonest of leafy liverworts, is shown in Fig. 330.

In all the liverworts thus far discussed and in fact in most liverworts, the sporophyte is parasitic upon the gametophyte, securing from it all its water and food. In striking contrast with these forms are the genus *Anthoceros* and two other closely related genera in which the sporophytes are green and able to carry on photosynthesis and thus to make their own food although they remain attached to the gametophyte and

are dependent upon it for their supply of water and of salts from the soil. These sporophytes possess stomata which are very like those of ferns and flowering plants. They have no seta but consist of a foot and a long cylindrical capsule which continues for some time to elongate by basal growth. Thus new spores are formed near the base while ripe ones are being discharged at the upper end where the capsule splits open. If these sporophytes only had rhizoids or roots by which they could absorb water and soil solutes directly from the soil, they would no doubt be able to carry on an existence quite independent of the gametophyte plants.

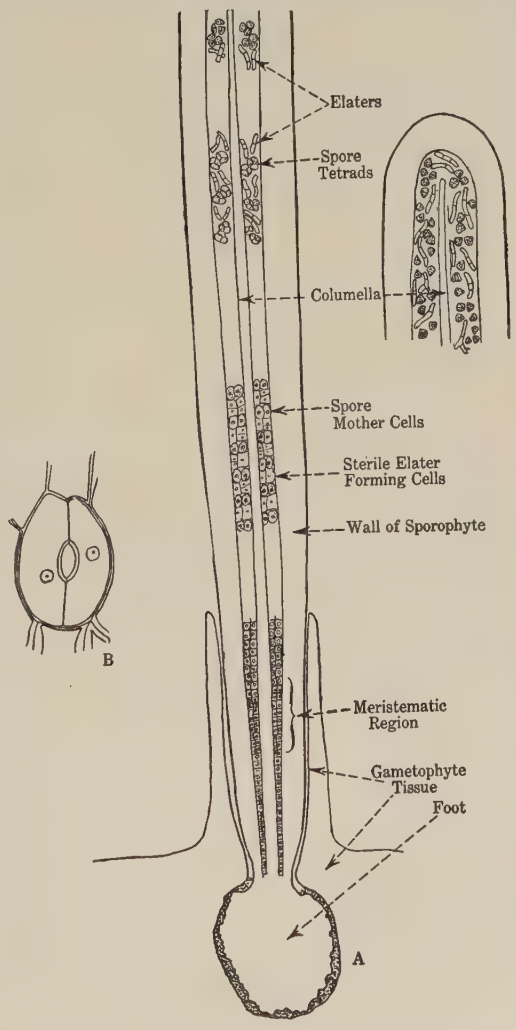


FIG. 332.—*Anthoceros*. *A*, diagram of a median longitudinal section of the basal portion of the sporophyte, including some gametophytic tissue to which the sporophyte is attached; and, to the right, the apical part of the sporophyte. *B*, a stoma and guard cells from the sporophyte.

THE MUSCI (MOSSES)

The second class of the Bryophyta includes many more genera and species than does the first class, the Hepaticae. Furthermore, the mosses are a much more conspicuous and important element of the flora than are the liverworts. There is, however, much more uniformity in the structure of both the vegetative and reproductive structures among the mosses than among the liverworts. The mosses

are not so strictly limited to very moist habitats as are most of the liverworts, and especially in northern countries large areas may be covered with an almost pure growth of mosses, whereas this is seldom true of the liverworts. A few mosses are aquatic, many grow upon soil, and many others grow upon rocks, the bark of trees, and decaying wood.

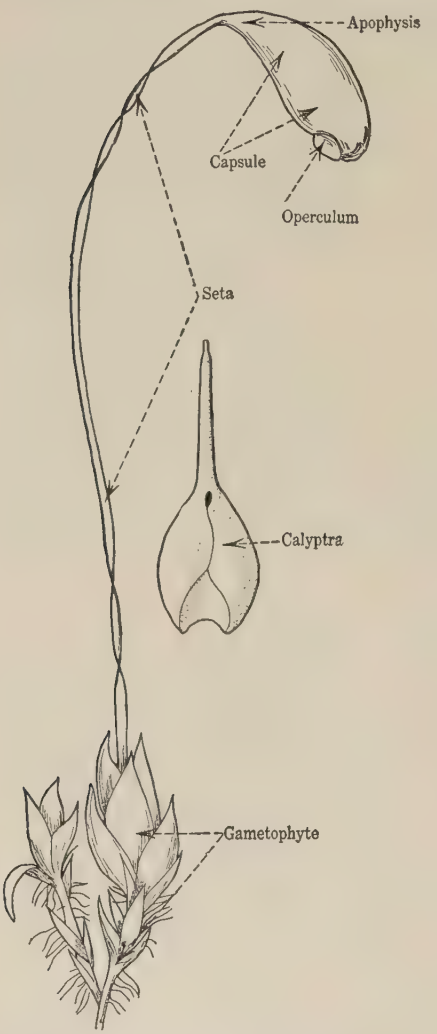


FIG. 333.—Portion of a gametophyte and attached sporophyte of a common moss, *Funaria hygrometrica*.

The mature gametophyte of the mosses always consists of a stem having rhizoids at the lower end and bearing spirally arranged leaves. These leaves differ from the leaves of the leafy liverworts, which are borne in two rows, not only in their spiral arrangement but also in having a midrib. With the exception of two genera, all of the mosses belong to a single order, the Bryales. A single life history will be sufficient to illustrate the principal features of the structure and development of the plants of this order.

FUNARIA

Germination of Spores and Development of the Gametophyte.—The spores of this plant, as of most of the mosses, are produced in large numbers, are very small, and are easily borne to considerable distances by the wind. In the woods where all the vegetation of a larger or smaller area has been destroyed by fires, this and other mosses often arise in great numbers before competing species of plants with less efficient methods of dissemination can secure a foothold. When

the spores germinate a leafy moss plant is not produced at once. Instead there develops a green filament made up of cells placed end to end as in many of the green algae. These cells have numerous conspicuous chloroplasts. As this green filament grows, it branches freely and under favorable conditions may cover a considerable area of the substratum. This alga-like growth is called **protonema** and is characteristic of all the mosses. The food which makes possible the growth of the protonema is mostly that formed by photosynthesis carried on by the protonema itself, for the quantity of food contained in the minute moss spore is very little.

The leafy moss shoots or **gametophores** (Fig. 333) arise from short branches of the protonema. Near the end of these branches an oblique wall is formed, cutting off an end cell. Two other oblique walls are soon formed. These cut the first wall and thus form an apical cell having the form of a three-sided pyramid of which the curved wall at the end of the branch forms the base. From this cell new cells are cut off by walls which are formed in succession parallel to the three sides of the pyramid. These daughter cells in turn undergo divisions and thus the tissue of the leafy shoot is formed. From the base of the gametophore numerous rhizoids grow out. These serve to attach the gametophore to the soil or other substratum and to absorb water and soil solutes. The rhizoids of mosses are not tubular outgrowths of superficial cells like those of most of the liverworts, but instead filaments of cells with cross walls which are often oblique. The rhizoids branch freely, and under favorable conditions they may give rise to a new protonema.

The leafy gametophores are what we speak of as moss plants and they are the most conspicuous part of the gametophyte. They are, however, in reality, simply branches of the gametophyte and many gametophores may arise from a protonema which has developed from a single spore. Within the stem and in the midribs of the leaf there are somewhat elongated cells which are apparently adapted for water conduction.

The gametangia (archegonia and antheridia) (Figs. 334 and 335) are produced in groups at the ends of the leafy shoots. Though formerly *Funaria* was believed to be dioecious, it has been shown that the gametophores which bear the antheridia develop first and that the shoots bearing the archegonia develop as branches of the same gametophores and may later become separated. There are, however, mosses which are truly dioecious. In these cases half of the spores produced give rise upon germination to a protonema which will produce only archegonia-bearing gametophores, while the remainder of the spores when

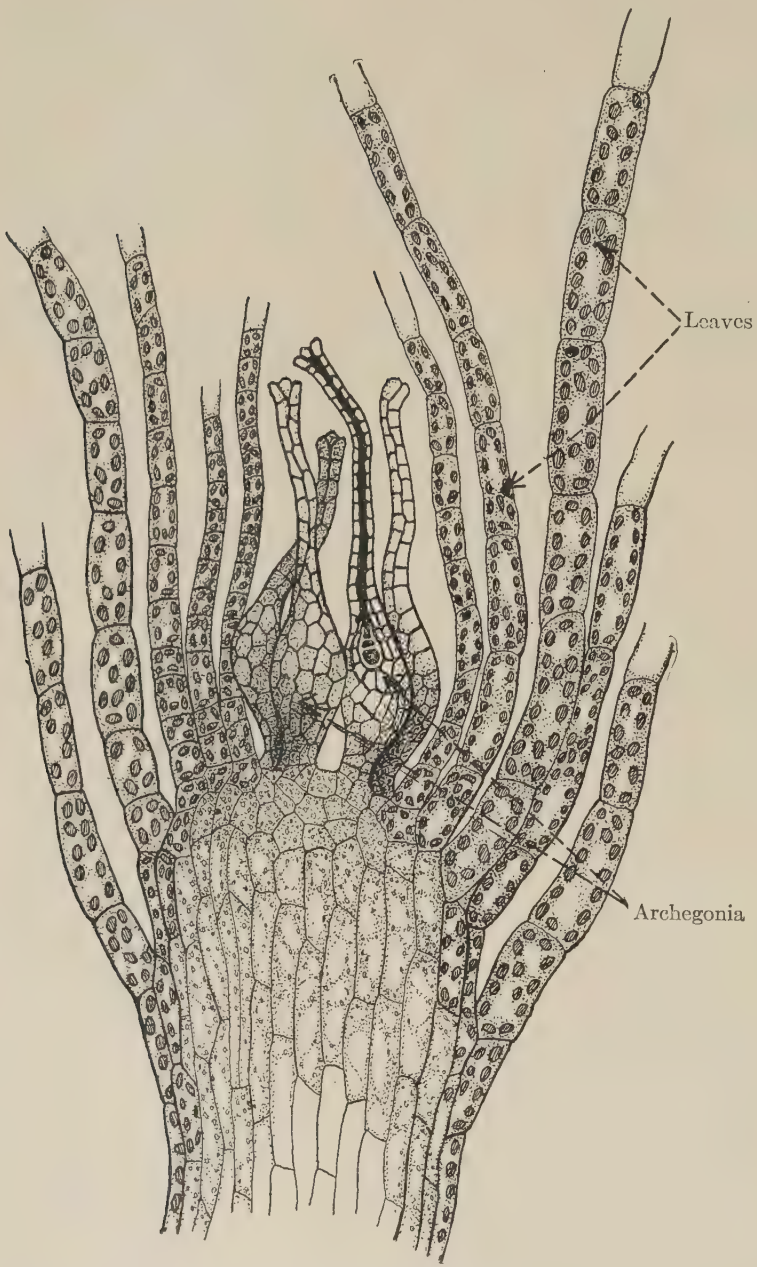


FIG. 334. —*Funaria hygrometrica.* Longitudinal section of tip of a female gametophore, showing archegonia. (Redrawn from Sachs.)

they germinate will form a protonema with antheridia-bearing gametophores. In *Funaria* the shoots bearing antheridia are easily recognized even without the use of a lens, for the leaves surrounding the terminal

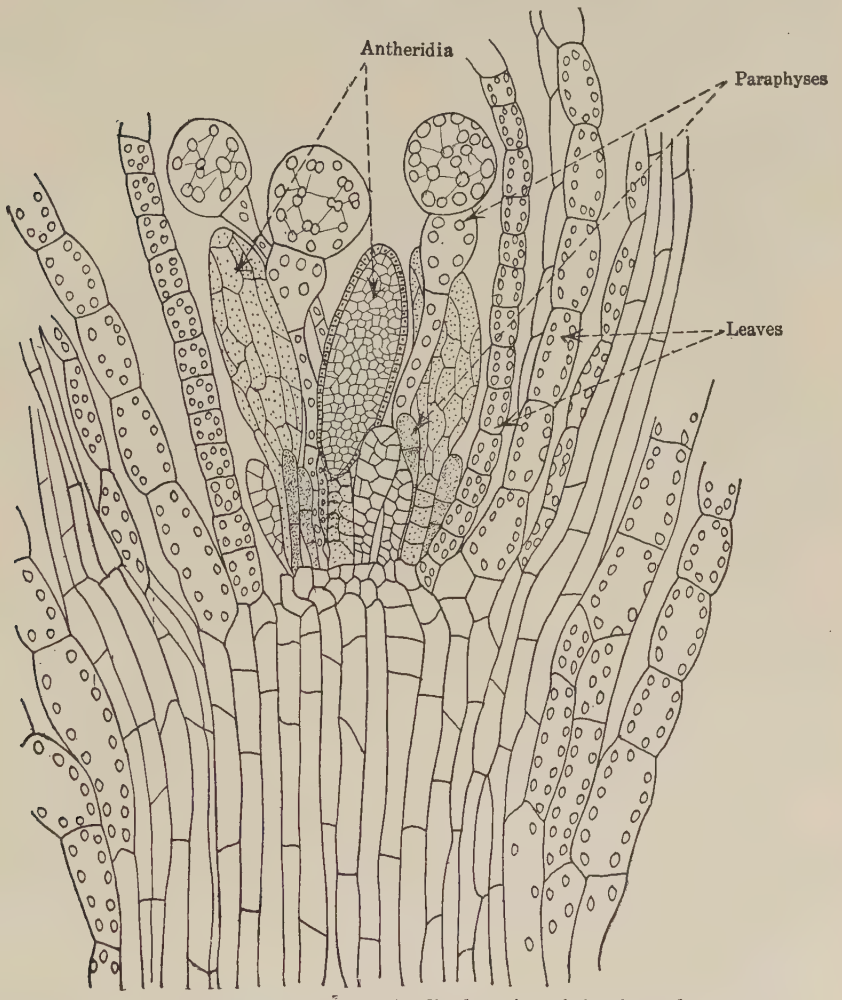


FIG. 335.—*Funaria hygrometrica.* Longitudinal section of tip of a male gametophore, showing antheridia and paraphyses. (Redrawn from Sachs.)

cluster of antheridia are spread somewhat like the petals of a flower. The group of antheridia can be seen as a distinctly orange spot in the center of the "flower." The leaves surrounding the archegonia overlap, giving the tip of the gametophore the appearance of a bud.

The Antheridia and Archegonia.—Although of distinctly dissimilar form from those of the liverworts, the antheridia of *Funaria* and other true mosses are essentially the same in structure as those of the liverworts. The cells forming the wall of the antheridium contain chloroplasts which become orange red (chromoplasts) when the antheridium ripens. The sperms are biciliate as in the liverworts. Among the antheridia grow club-shaped, multicellular sterile hairs or paraphyses with conspicuous chloroplasts (Fig. 337). Paraphyses of a different type are found among the archegonia.

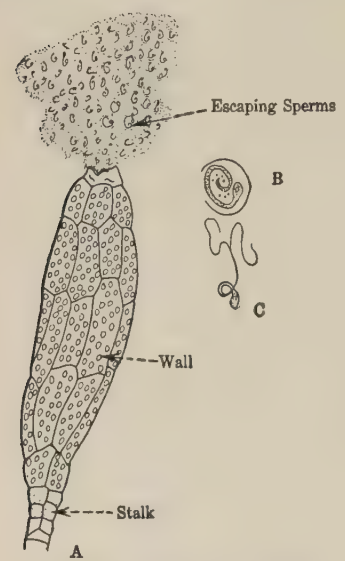


Fig. 336.—*Funaria hygrometrica.* *A*, mature antheridium discharging its sperms. These are at first held together by mucilage from the disorganized walls of the sperm-producing cells. *B*, a sperm still held in the mucilage. *C*, a sperm free from the mucilage. The chromoplasts shown in the wall cells of the antheridium (*A*) are orange in color.

Fig. 337.—A single paraphysis from a group of *Funaria* antheridia. The oval bodies in the cells are chloroplasts.

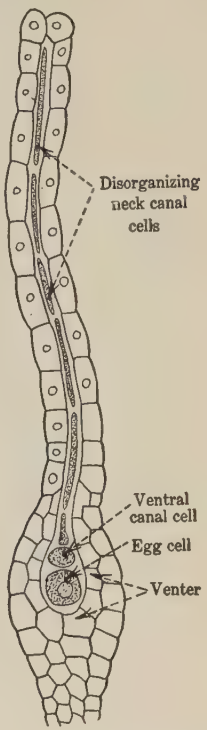


Fig. 338.—A mature archegonium of *Funaria.*

The archegonia have a conspicuous stalk. Though essentially the same in structure they differ from the archegonia of the liverworts in having a longer neck and a larger number of neck canal cells (Fig. 338).

As in the liverworts, the opening of the antheridia and archegonia as well as the accomplishment of fertilization can take place only when the plants are wet. It has been shown that, in some mosses at least, the sperms are chemotactic toward certain substances, cane sugar for example, given out from the open archegonium. This is probably also the case in *Funaria*.

The Sporophyte.—It will be recalled that all that portion of the life cycle from the first division of the spore mother cells to the fusion of the gametes in the process of fertilization belongs to the gametophyte generation or phase. The nucleus of the moss spore and the nuclei of the cells of the protonema, gametophores, and gametangia and the nuclei of the gametes have the haploid chromosome number. The fertilized egg cell or zygote, however, has the diploid chromosome number since it contains chromatin derived from the two gametes.

Immediately after fertilization the naked zygote of *Funaria* produces a cellulose wall about itself and the formation of an embryo sporophyte begins. Growth and repeated cell divisions result in the formation of a spindle-shaped embryo with an apical cell at the upper end (Fig. 339). As this continues to grow the venter of the archegonium keeps pace with it, forming an envelope called the calpytra. Soon there begins a differentiation of the embryo sporophyte into foot, seta, and capsule. The foot penetrates the tissue of the apex of the gametophore as in *Marchantia* and most other liverworts. The seta becomes long and slender and within it there is differentiated a central strand of elongated cells. It is when the seta elongates very rapidly, a short time before maturing of the sporophyte, that the base of the calyptra is torn away from the gametophyte. It remains for some time as a cap or hood over the capsule.

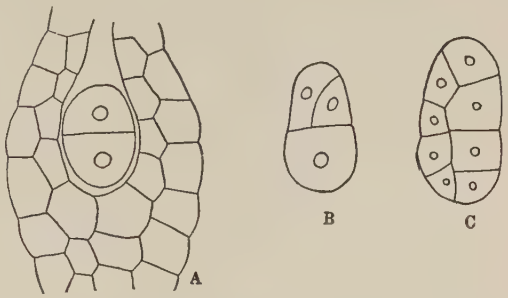


Fig. 339.—Early stages in the development of the sporophyte of *Funaria* from the zygote. *A*, after the first division of the zygote, the two-celled embryo still within the venter of the archegonium. *B* and *C*, later stages; in these the archegonium venter has not been shown. (*C*, drawn from a preparation of D. H. Campbell.)

The capsule of *Funaria* and related mosses is a structure of much greater complexity than any yet met with among liverworts and mosses. It is approached in this respect only by the capsule of *Anthoceros* and a

few closely related genera. It has a definite epidermis with stomata, very similar to those of the sporophytes of the ferns and flowering plants, a layer of chlorenchyma, and a complicated provision for opening the capsule and scattering the spores. The part of the capsule devoted to spore production is relatively very small. Figure 341 shows the principal features of the anatomy of a mature capsule from which the calyptra has been removed. The outer layer of tissue is the epidermis, the cells of which have much thickened outer walls as in the flowering plants. It is in the epidermis of the **apophysis** (basal portion of the capsule) that stomata are found. In early stages of their development the stomata are similar in structure to those of the flowering plants, although when they are fully developed the cavities of the guard cells communicate with each other. Underneath the epidermis are several layers of wall cells, and next to this a zone of very large intercellular spaces crossed by branched filaments of green cells. The center of the upper part of the capsule is made up of a more or less cylindrical mass of delicate, colorless, parenchyma cells called the **columella.** Just outside the columella is a narrow zone of sporogenous tissue and between this and the loose chlorenchyma are several layers of compact cells which supply food to the developing spores. It will be seen from the figure that the quantity of

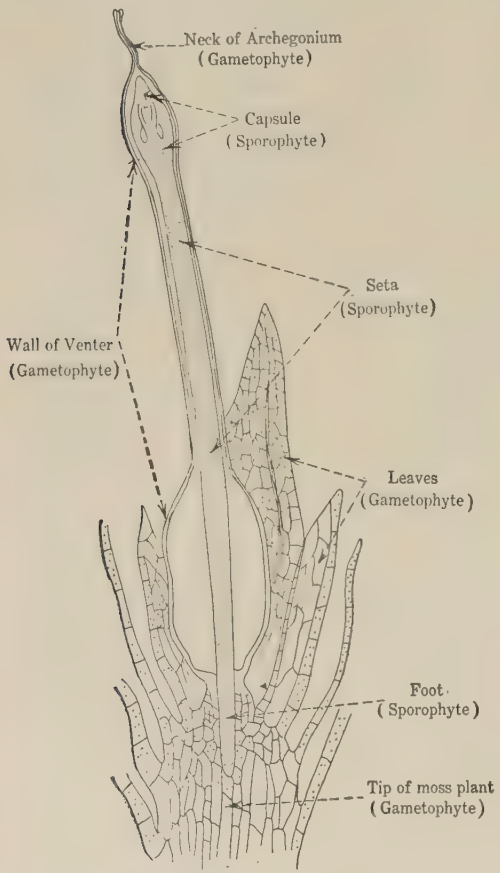


FIG. 340.—Tip of a female gametophyte branch and advanced sporophyte as seen in longitudinal section (semi-diagrammatic). The shaded structure is the sporophyte. (Adapted from Sachs.)

sporogenous tissue is very small as compared with the sterile tissue. As in the liverworts and in practically all of the ferns and their allies, and in the flowering plants as well, the spores are produced in tetrads, or groups of four. Each such group of four spores is derived from a single spore mother cell. Their formation is preceded by two nuclear divisions, of which the first is a reduction division. The spore mother cell is the last stage in the life cycle in which the chromosome number is diploid; it is the end of the sporophyte generation, and accordingly the spore nuclei are haploid.

The upper end of the columella is a dome-shaped mass of parenchyma cells which projects out from the main mass of the capsule. This part of the columella is not surrounded by a layer of sporogenous tissue but by several layers of sterile cells which form two peculiar structures, the **operculum** and the **peristome** (Fig. 341). The operculum is a cap made up of the four or five outermost layers of cells. When the capsule is mature and begins to dry up, the operculum is loosened from the tissues beneath it by a breaking down of certain thin cell walls, and it soon falls off. Later a double fringe of long triangular teeth, the peristome, is formed by radial and tangential splitting of the layer of tissue just below the operculum and just outside the rounded extremity of the columella. The edge or rim of the capsule to which these teeth are attached is made up of thick-walled cells and is called the **annulus.** By the time the spores are ripe and the operculum has been lost, most of the thin-walled cells within the capsule, including those of the colu-

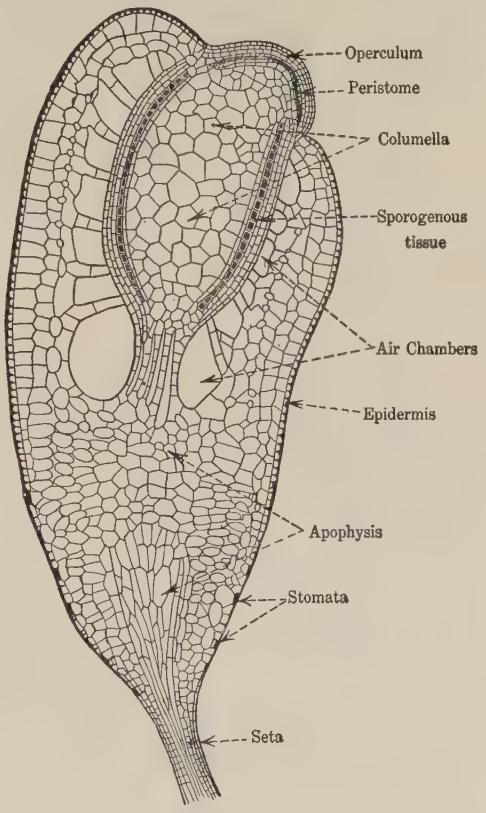


FIG. 341.—Longitudinal section of the capsule of the sporophyte of *Funaria hygrometrica.*

mella, collapse, leaving a cavity which is filled with a loose mass of spores. The peristome teeth are rough by reason of the attached fragments of cell walls and they are highly hygroscopic. When they are wet or the atmospheric humidity is very high, the peristome teeth bend inward and reach into the cavity of the capsule. When they become dry they straighten out and lift out some of the spores which then are disseminated by air movements. If these spores come to rest on a moist substratum and if the conditions of illumination and temperature are favorable, they germinate and form a protonema as already described.

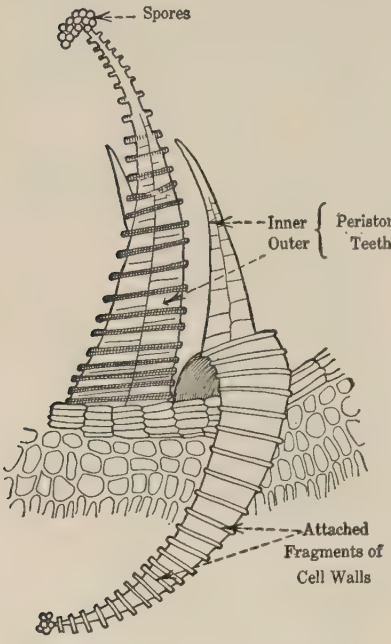


FIG. 342.—A portion of the peristome of a *Funaria* capsule, showing several of the inner and of the outer peristome teeth.

The Life Cycle. A Summary.—The life cycle of *Funaria* may be summarized in a few brief statements:

1. Germination of the spores from which results the development of a branched filamentous, alga-like growth called the protonema.

2. The formation of special protonema branches, and the setting up of an apical cell at the end of each branch.

3. The growth of each of these special branches or "buds" into a gametophore, consisting of a stem bearing rhizoids at the lower end and simple leaves above.

4. The formation at the tip of some of the leafy shoots or gametophores of groups of antheridia mixed with paraphyses.

5. The formation at the tips of other gametophores (originating in *Funaria* as branches of the antheridia bearing gametophores) of groups of archegonia mixed with paraphyses.

6. The opening of antheridia and archegonia during a period when the plants are wet. There results the clearing of the archegonium neck canal of all obstruction to the entrance of sperms and the escape of the sperms from the antheridia.

7. Swimming of some of the sperms to the archegonia whither they

are probably directed by certain substances (cane sugar in some cases), which diffuse outward from the open archegonia.

8. Fertilization, followed by the formation of a cell wall about the zygote. This ends the gametophyte or haploid phase.

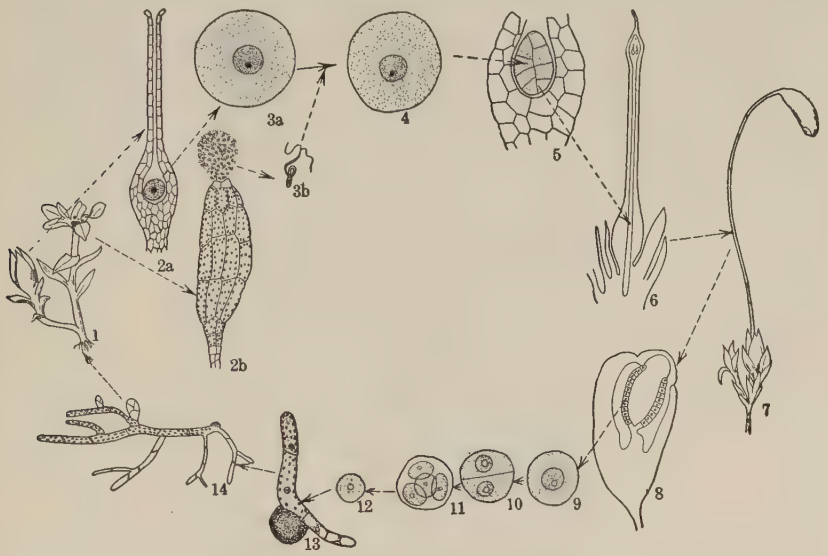


FIG. 343.—Diagram showing the life cycle of a typical moss (*Funaria*). 1, the leafy gametophyte plant (gametophore), showing an antheridial and an archegonial branch. 2*a* and 2*b*, an archegonium and an antheridium with mature egg and sperm. 3*a* and 3*b*, an egg and a sperm. 4, the zygote resulting from their fusion. 5, a young embryo sporophyte within the venter of the archegonium. 6, sporophyte in advanced stage of development, attached to the gametophyte and surrounded by the enlarged archegonium. 7, mature sporophyte attached to the gametophyte. 8, section of the sporophyte capsule showing the location of the spore mother cells. 9, spore mother cell. 10, two cells resulting from reduction division of the spore mother cell. 11, tetrad of spores resulting from division of the two cells. 12, a single spore. 13, germinating spore showing protonemal thread and rhizoid. 14, older gametophyte plant showing the buds which develop into leaf shoots of the gametophyte. The stages from 4 to 9 belong to the sporophyte generation. Those from 10 to 3 to the gametophyte generation.

9. The development of the zygote by growth and cell divisions into an embryo sporophyte which is enclosed by the enlarged archegonium venter (calyptra) until just before the maturity of the sporophyte when the calyptra is torn away from its attachment to the leafy shoot.

10. The development of the embryo into the mature sporophyte consisting of (*a*) the foot which penetrates the tip of the stem of the gametophore and serves as an organ of attachment and absorption, (*b*) the seta or stalk and (*c*) the capsule, a complex structure within which the spore mother cells are produced but which is mostly made up of sterile tissue.

11. The two successive divisions of each spore mother cell to form a tetrad of spores. The first division of the spore mother cells marks the

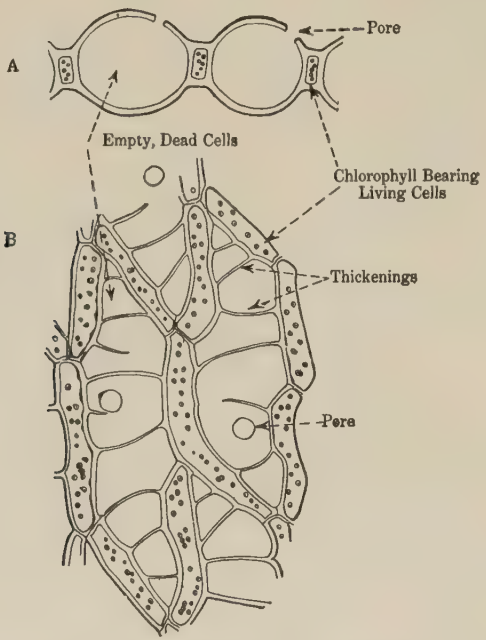


FIG. 344.—Sphagnum moss. *A*, portion of leaf in cross section; *B*, portion of leaf in surface view.

end of the diploid or sporophyte phase and the beginning of the haploid or gametophyte phase.

12. The drying out of the capsule, the loss of the operculum or capsule cover, and the escape, assisted by the hygroscopic movements of the peristome teeth, of the spores.

In Fig. 343 the life cycle of such a moss as *Funaria* is represented in the form of a diagram.

THE SPHAGNUMS

Distinctly different from *Funaria*, which is typical of most mosses, are the sphagnums or peat-mosses. These belong to a single genus and are mostly restricted to the swampy land in the vicinity of northern lakes where they often cover large areas and form "peat-bogs." The gametophores are of a much paler color than those of the common mosses. When dry they can absorb great quantities of water or other liquids. This fact led to the use of dry sphagnums during the late war as a substitute for absorbent cotton in certain kinds of surgical dressings.

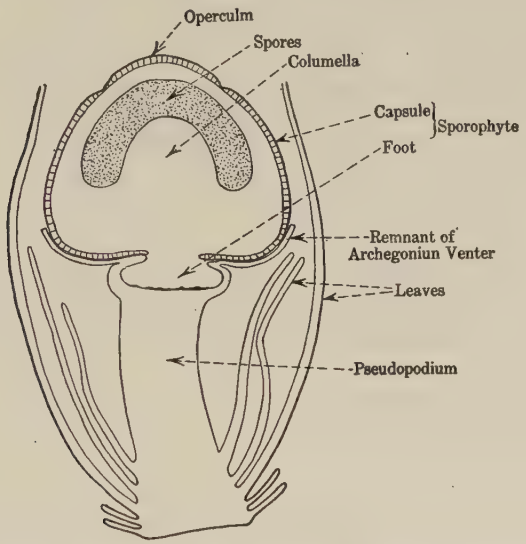


FIG. 345.—A mature sporophyte of *Sphagnum* in longitudinal section showing its attachment to the tip of the gametophyte branch.

The principal particulars in which the members of the genus *Sphagnum* differ from such common mosses as *Funaria*, are:

1. The protonema is an irregular flat thallus instead of a system of branching filaments.

2. Most of the leaves, except when very young, consist of a network of small chlorophyll-bearing cells, the spaces between which are filled by large empty cells which generally have a circular opening in the cell wall (Fig. 344). It is these large colorless cells which are responsible for the light green color of the leaves and it is chiefly because of the presence of these large empty cells that dry sphagnum has so great a capacity for the absorption of liquids.

3. The sporophyte has no seta but is raised somewhat by the elongation of the gametophore stem below the region to which the foot is attached. The sporogenous tissue surrounds not only the sides of the columella but the upper end as well.

SUMMARY OF THE BRYOPHYTA

The forms which have been described in this chapter do not represent successive stages in evolution. They do, however, illustrate in all probability some of the principal steps which took place in the evolution of the sporophyte. The following is a summary of the most significant facts to be learned from a brief study of the Bryophyta:

1. Although certainly not aquatic plants like their ancestors, the algae, the Bryophyta show clear evidence of their origin from aquatic plants and of their incomplete adaptation to life on land.

2. The single most important distinction between these plants and the algae is the alternation in the life cycle of all of them of a sexual generation with haploid nuclei and an asexual generation with diploid nuclei.

3. The adoption of a land habitat by these plants has necessitated certain structural and physiological adaptations in response to the great difference in the environment of land plants and that of submerged aquatics.

(*A*) The most important points of difference between the aquatic and the terrestrial habitats are:

(*a*) That on land only part of the plant is in contact with a medium (the soil) from which it can absorb water and essential salts.

(*b*) That the land plant is partly exposed to a medium (the atmosphere) to which it is almost continuously losing water.

(*c*) That whereas aquatic plants (submerged) are largely supported (buoyed up) by reason of the high specific gravity of water, the atmosphere does not yield land plants any appreciable mechanical support.

(*d*) That on account of the low specific gravity of the atmosphere it is a less efficient agency for distribution of gametes and spores than is water.

(*B*) Some of the principal characteristics of the Bryophyta and of higher land plants which are apparently related to these differences in environment are:

(*a*) Special structures for the absorption of water and minerals from the soil are developed by all typical land plants—the rhizoid of lower land plants (Bryophyta) and the roots and root hairs of ferns and flowering plants. The rhizoids of the Bryophyta are, however, not very efficient organs for water absorption.

(*b*) The parts exposed to the air are protected from excessive water loss by the production of a superficial layer (epidermis) having an outer wall which, with its cuticle, is very resistant to the passage of water vapor. It is important that this should not prevent the entrance of the gases needed for photosynthesis and respiration. The epidermis among the higher plants, accordingly, has openings through it, called stomata. In all but the smallest land plants there are conductive tissues which provide for the rapid transfer of water from the water absorbing structures to the parts exposed to the dry atmosphere.

(*c*) The more primitive land plants either grow prone upon the ground or, if erect, seldom attain a height of more than a centimeter or two, since they are lacking in mechanical tissue. Higher land plants have developed mechanical tissues and some of them are able to support a stem hundreds of feet high.

(*d*) In the Bryophyta and in the Pteridophyta as well, fertilization can take place only when the gametophytes are wet, because the sperms can move only in water. By various means the spores of land plants are adapted to efficient dissemination by air instead of water. Small size and the development of ridges or spines on the outer spore wall are among the principal means used. The discharge of spores into the air from elevated structures, such as the long-stalked capsules of the mosses and many liverworts, makes it more likely that they will be carried to some distance by air currents before they fall to the ground.

4. In all the Bryophyta the gametophyte is " the plant," that is to say, the gametophyte is the conspicuous and independent plant, which alone is able to absorb water and to which the function of food manufacture is entirely or largely restricted. It is among the Bryophyta (in *Marchantia* and similar liverworts and in the mosses) that the gametophyte reaches its highest development among plants. There is a well-developed epidermis with specialized air pores in *Marchantia*, and

rudimentary conductive tissue in the mosses. The gametophyte at its best, however, never becomes an efficient land plant.

5. Among living bryophytes the sporophyte ranges in complexity from that of *Riccia*, which consists of a mass of spores with a single surrounding layer of sterile cells and which has no provision for spore dissemination, to the complex sporophyte of the mosses, in which sporogenous tissue is much reduced and tissues for photosynthesis and elaborate provision for spore dissemination are present. However, the sporophyte's possibilities of development are limited by reason of the fact that it is restricted in the quantity of water and salts it can secure by the limited ability of the gametophyte for absorption and conduction.

6. In the next class, the Pteridophyta, the gametophyte is even simpler than in the Bryophyta, but the sporophyte is much more complex than in the mosses and liverworts. Moreover, it develops entirely new sporophyte organs, a root and a stem with leaves. The presence of a root makes it possible for the sporophyte to secure adequate supplies of water and salts, and thus to become a structure of great size and complexity.

CHAPTER XIV

PTERIDOPHYTA (FERNS AND FERN ALLIES)

GENERAL CHARACTERISTICS

The ferns and their allies constitute a large assemblage of plants which have certain resemblances to the liverworts and mosses on the one hand, and to the seed plants on the other. They resemble the Bryophyta in the following important particulars: (1) They produce ciliated male gametes; (2) they require water in order that fertilization may take place; and (3) they have gametangia which are essentially of the same structure as those of the liverworts and mosses. They resemble the Spermatophyta in that their sporophytes all have roots and can therefore live independent of the gametophyte, and in that they possess well developed vascular tissue.

We have seen that in the Bryophyta the sporophyte is entirely dependent for its supply of water and mineral salts upon the gametophyte, which alone possesses organs (rhizoids) for absorbing water and soil solutes from the soil. In many of the Bryophyta the sporophyte is unable to manufacture any of its own food, even when supplied by the gametophyte with these raw materials. But there is a certain approach to independence of the sporophyte in *Anthoceros* and in most mosses which have developed chlorophyll-bearing tissue and which could probably live entirely independently if they possessed rhizoids or a root.

It is within the Pteridophyta that complete independence of the sporophyte is first attained. Although the sporophyte of the ferns and fern allies is at first attached to the gametophyte by a foot and is for a short time dependent upon it for water and food as well, it soon develops a root which attaches it directly to the soil. By virtue of having a root, the sporophyte is no longer dependent upon the gametophyte for its supply of water and mineral salts. Moreover, food-manufacturing tissue is well developed in the sporophyte, so that this generation has attained complete independence.

The Pteridophyta have carried tissue differentiation in the sporophyte much further than any of the Bryophyta. The sporophyte has among other specialized tissues, a well-organized vascular system.

This, together with an efficient epidermis, abundant chlorenchyma, and a root which can penetrate into the deeper and relatively moister layers of soil, has enabled it successfully to carry on an independent terrestrial existence, which is not possible for the sporophyte of any of the Bryophyta.

The roots of the Pteridophyta and Spermatophyta, although performing the same functions as rhizoids, are far more complex structurally and are capable of indefinite growth.

As to the origin of the Pteridophyta, it is the generally accepted opinion that they and the mosses represent two distinct lines of development from some liverwort ancestor. The Bryales have the most complex and highly differentiated sporophyte of any existing plants below the Pteridophyta, but there is little ground for the assumption that the Pteridophyta have arisen from the mosses even though the mosses are in some respects intermediate between the liverworts and the ferns.

A study of fossil plant remains reveals the fact that the ferns and their allies appeared on the earth earlier than the seed plants. During the carboniferous period (geological age when the great coal beds were deposited) they were very abundant; in fact they dominated the vegetation of that time.

The Pteridophyta which exist upon the earth to-day are divided into three classes:

1. The Filicineae (Ferns)
2. The Equisetineae (Horsetails)
3. The Lycopodineae (Club Mosses).

THE FERNS (FILICINEAE)

A large majority of living pteridophytes belong to the Filicineae, of which two sub-classes are recognized: (1) the **eusporangiate** ferns in which the spore cases (sporangia) have walls which are several layers of cells thick and in which the spore-producing cells originate below the epidermal layer; and (2) the **leptosporangiate** ferns in which the spore cases have walls of one cell layer and the whole sporangium with its spores develops from a single projecting superficial cell. The eusporangiate ferns are a small group which had many more representatives in earlier geological periods than now. The adder's tongue fern (*Ophioglossum*), the moonwort (*Botrychium*), and certain large tropical ferns of the family Marattiaceae are examples of eusporangiate ferns. The leptosporangiate ferns are the common ferns of woodland, garden, and conservatory.

Distribution and Habitat.—Ferns are widely distributed over the surface of the earth. They flourish most luxuriantly in moist, shady

habitats, but there are some species which grow in very dry situations. Ferns reach their greatest size in the tropics, where certain tree ferns grow to a height of fifteen meters or more. The stems of such tree ferns are erect, woody, and unbranched, and each bears at its apex a cluster of compound leaves (fronds). Most of the ferns, however, have

FIG. 346.—Sporophyte of Christmas fern (*Polystichum*), showing the horizontal rhizome bearing at the tip young coiled leaves, the expanded leaves of the previous season, each with a stalk or stipe prolonged to form the rachis from which pinnae (leaflets) arise laterally, and the fibrous roots which arise from the lower side of the rhizome. The older parts of the stem are covered with the petioles of dead leaves. (After Curtis.)

a horizontal or short erect stem (rhizome) which is developed underground.

Life History of Polypodium.—This leptosporangiate genus is selected as a type for detailed discussion because it is widely distributed and its life history is quite representative of the ferns with which we are most familiar.

The familiar fern plant, as we know it, with its roots, stem and leaves (fronds) is the asexual or sporophyte generation. The cells of this

generation have nuclei with the diploid ($2x$) number of chromosomes. The sexual or gametophyte generation is a small independent plant which is devoid of roots, stem and leaves, is seldom more than a few millimeters in diameter, and is even simpler in structure than the gametophytes of mosses and most liverworts. It is often spoken of as a **prothallium** (Fig. 348). The cells of the gametophyte generation have nuclei with the haploid (x) number of chromosomes.

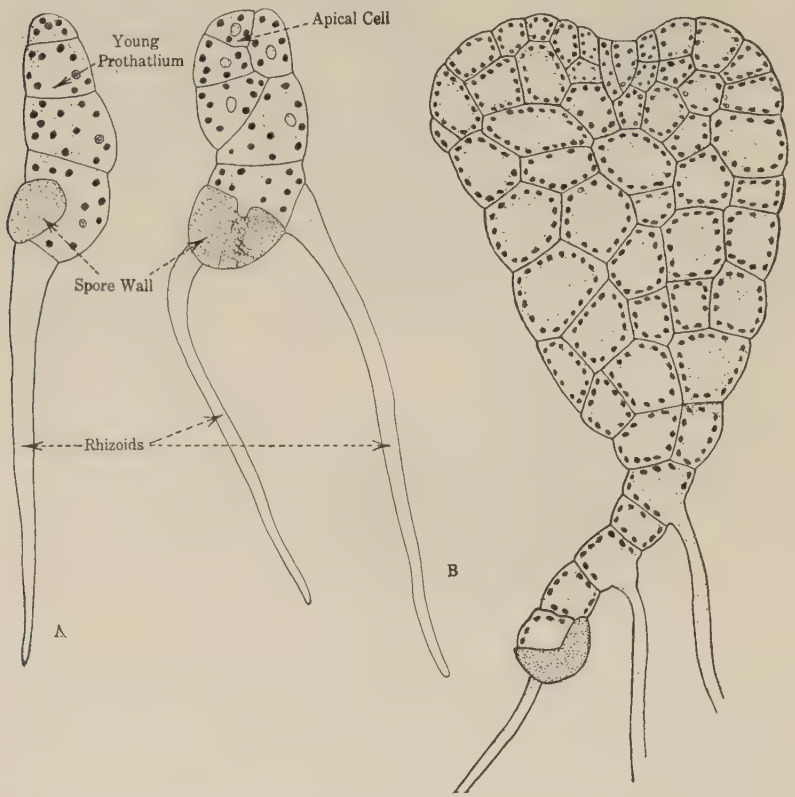


FIG. 347.—Early stages in the development of the gametophyte of *Polypodium*. (See explanation in text.)

Spores.—There often occur, on the under side of the frond, brownish "dots," which are clusters of sporangia or spore cases. Within each of these cases there are a number of spores. The spores have the haploid number of chromosomes and, accordingly, belong to the gametophyte generation.

In *Polypodium* all the spores are similar in size and appearance, and

accordingly *Polypodium* is said to be **homosporous,** in contrast to those pteridophytes which produce two kinds of spores differing in size and in other respects and which are therefore said to be **heterosporous.**

Spore Germination.—The spores of *Polypodium* have two coats or wall layers. The outer layer (exine) is hard, brown, and rough; the

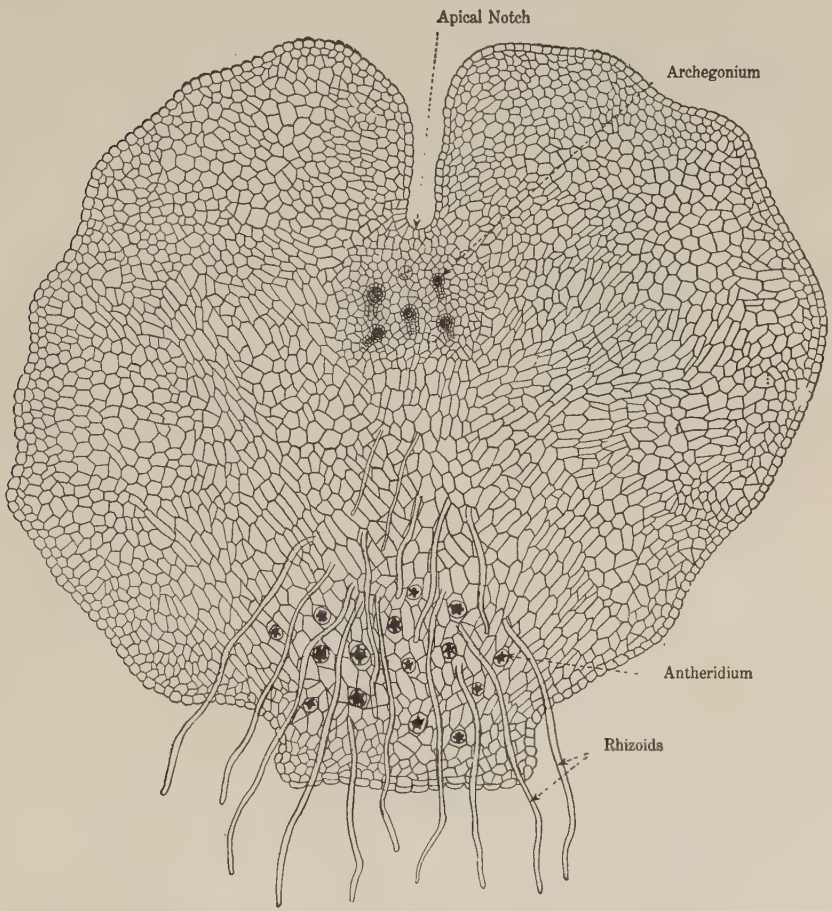


Fig. 348.—Mature gametophyte (prothallium) of fern, as seen from the ventral surface.

inner (intine) is thin and delicate. Under favorable conditions of moisture and temperature, water is absorbed by the spore, the exine is ruptured, and the spore contents, surrounded by the intine, protrude as a short tube.

This germination tube is cut off by a cell wall as a stout, green

cell, at the base of which the first rhizoid appears. By rapid growth, the cell elongates, and soon by divisions in one plane, comes to form a row of green cells.

The Gametophyte (Prothallium).—After a time, the terminal cell of this short filament becomes divided by an oblique wall. This division is succeeded by the formation of a similar oblique wall in the larger of the two resulting cells. There is thus formed a triangular apical cell with two cutting faces. By the divisions of this apical cell the prothallium develops into a flat, green plate of cells. If growth is unhampered, the structure becomes more or less heart-shaped, with the apical cell at the bottom of the notch. During its growth, many unicellular rhizoids are developed on the under (ventral) surface. The mature gametophyte is one layer of cells in thickness, except in a region just back of the apical notch, where a cushion of cells is formed.

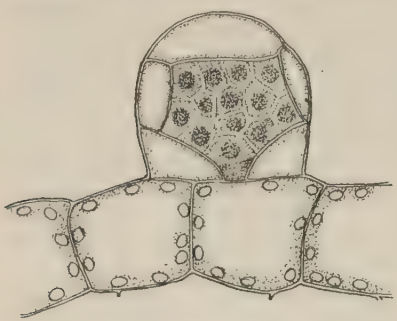


FIG. 349.—Mature antheridium of a true fern. (After Atkinson.)

In *Polypodium* and in most other ferns, each prothallium bears both antheridia and archegonia; that is to say, most ferns are monoecious. Some species, however, have the male and female gametangia on different gametophytes, that is, are dioecious. In dioecious ferns, such as *Onoclea*, the antheridia-bearing or male gametophytes are frequently smaller than the archegonial or female gametophytes.

The gametangia are borne on the ventral surface of the gametophyte, the antheridia being scattered among the rhizoids, and the archegonia are located just below the apical notch, where the prothallium is several cells thick. The antheridia develop earlier than the archegonia.

Antheridia.—The antheridium is spherical in shape and is not stalked, as are the antheridia of the Bryophyta. It consists of a single layer of chlorophyll-bearing cells, enclosing sperm mother cells, usually thirty-two in number. Each of these sperm mother cells develops into a sperm, a spirally-coiled structure consisting mostly of nuclear material, and bearing, not two cilia, as in the Bryophyta, but a large number.

Archegonia.—The archegonium is a flask-shaped structure resembling that of the bryophytes except that it is shorter and that the venter is embedded in the tissue of the gametophyte. There is one long neck-canal cell, below which is a single ventral-canal cell, and a large egg cell. At maturity, the neck-canal cell and ventral-canal cell

disintegrate into a mucilaginous mass, and a passageway is formed to the egg.

Fertilization and Embryo Development.—The rupturing of the archegonia and antheridia takes place only in the presence of water, as described in the case of Bryophyta; the mucilaginous material in the neck-canal cell of the archegonium swells and the cover cells open. The sperms are set free from the antheridia in the presence of water. They swim to the neck of the archegonium, and move down the neck-canal to the egg. A number of sperms may be attracted to one archegonium and may pass down the neck-canal, but only one fuses with the egg. The zygote (oöspore) remains in the venter and germinates there.

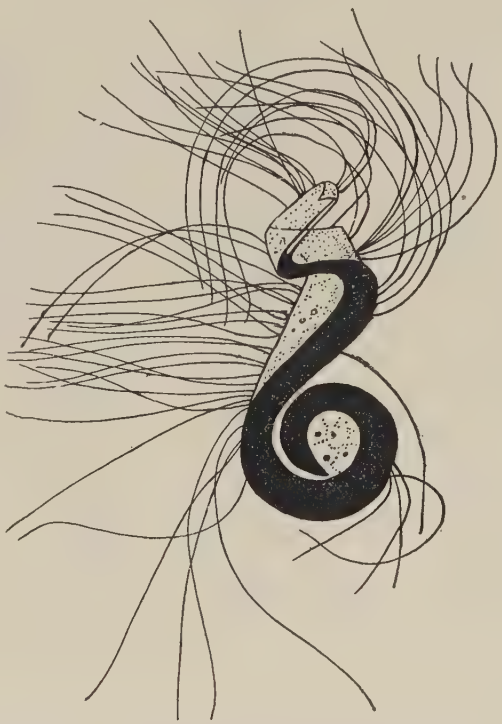


FIG. 350.—*Onoclea struthiopteris*. Ripe sperm, the nucleus black. (After Steil.)

It has been shown that the principal substances which attract the sperms to the egg in the species studied are malic acid and its salts.

FIG. 351.—Mature archegonium of a true fern.

At fertilization, the number of chromosomes is doubled so that the zygote has the diploid number, and hence belongs to the sporophyte generation.

Following fertilization the zygote begins its development into "the fern plant" (sporophyte). It forms a wall about itself and by two successive divisions becomes a four-celled body. This is spoken of as the **quadrant** stage of embryo development. From these four quadrants, four distinct primary growing points are formed, from

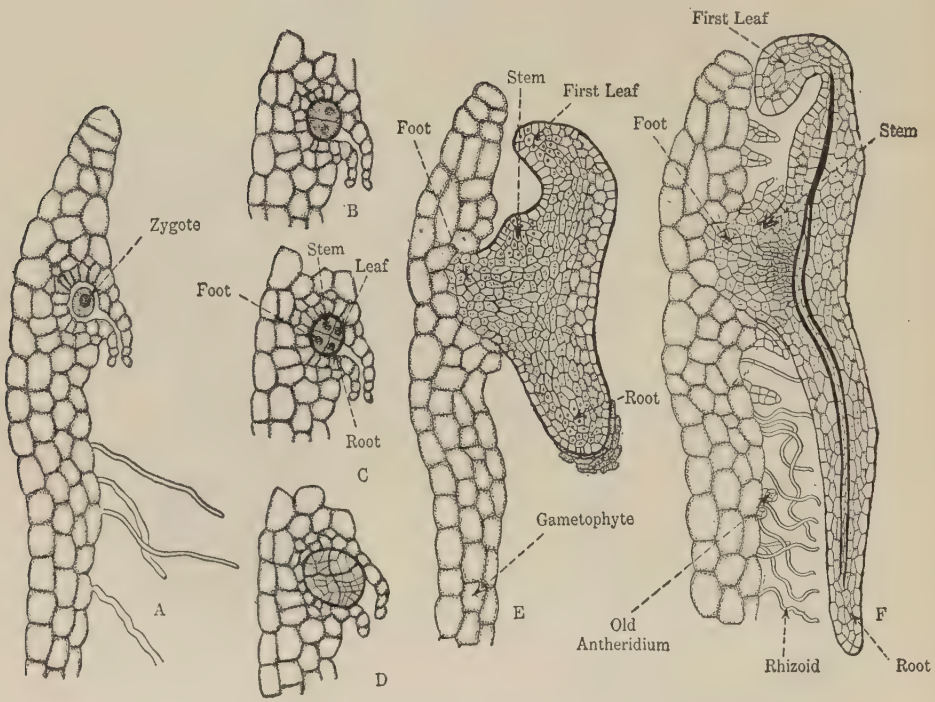


FIG. 352.—Stages in the development of the fern sporophyte.

which are developed the following distinct primary organs of the embryo:

1. *The foot*, which is a mass of small cells embedded in the tissue of the prothallium, and which absorbs food and water for the young embryo.

2. *The root*, which pushes its way into the soil.

3. *The primary leaf*, which, though little resembling the permanent leaves, is the first photosynthetic organ of the sporophyte.

4. *The stem*, which becomes the perennial rhizome from which the fronds and adventitious roots arise.

These organs develop in the order given. In the early stages of embryo development, the young sporophyte is completely parasitic upon the game-

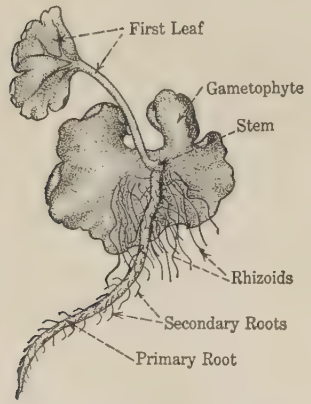


FIG. 352 (continued).—Fern sporophyte after its root has entered the soil and its first leaf has begun to carry on photosynthesis but before the death of the gametophyte.

tophyte, just as in the case of the liverworts, obtaining its food and water through the foot. However, as soon as the primary root and leaf are developed, it becomes an independent organism. The gametophyte soon withers and then the foot ceases to function. Of the four structures mentioned only the stem (rhizome) is permanent. It soon develops leaves and adventitious roots, and the primary root and primary leaf die.

The Mature Sporophyte. The Stem (Rhizome).—In *Polypodium*, as in most common ferns of temperate regions, the stem is subterranean and generally grows horizontally a few inches beneath the surface of the ground. It usually branches sparingly, and at the free ends are the growing apices (buds) which are protected, as a rule, by a dense growth of scales and epidermal hairs. Increase in length of the rhizomes continues from year to year by growth from these terminal buds. Hence, the rhizome is perennial. Each year new adventitious roots arise from the lower side of the rhizome and new leaves from its upper side. The leaves generally die at the close of each growing season. Examination of the older portions of the stem shows them to be covered by the bases of the petioles of dead fronds. By the death of older parts of the rhizome, branches become disconnected from the main rhizome and continue their development as separate new plants. In this way vegetative reproduction is accomplished. Ferns are propagated commercially chiefly by division of the rhizome.

The stem of ferns is much more complex in structure than any organ found in the Bryophyta. Its outstanding structural feature is a water and food-conducting system (vascular system). A cross section through the internode of the rhizome of *Polypodium* shows the following tissues:

1. *Epidermis.*—This consists of a single layer of thick-walled cells.

2. *Sclerenchyma.*—Just beneath the epidermis are several layers of **sclerenchyma** cells, and there are two or three distinct masses of this tissue nearer the center of the stem.

3. *Vascular Bundles.*—A varying number of these, some large and some small, are found near the center of the stem. They are separated from each other, and each is surrounded by an **endodermis.** The vascular bundles possess both xylem and phloem, but no cambium. They are of the **concentric type,** that is, the phloem surrounds the xylem. The vascular bundles extend throughout the leaves and roots.

4. *Parenchyma Tissue.*—This forms the ground tissue of the stem. The principal function of this tissue is storage of food and water.

The Root.—The roots are small and fibrous, and except for the primary root, which soon dies, all roots are adventitious and arise from

the lower side of the stem. They have an endogenous origin, as have the roots of seed plants. The roots have root hairs, a root cap, and a single vascular bundle of the radial type.

The Leaf.—The frond of *Polypodium* and most common ferns consists of a stalk or **stipe,** which is prolonged to form the **rachis,** from which arise laterally a number of **pinnae** (leaflets). Leaf primorida may be observed as small swellings near the growing point of the rhizome. These leaf primordia grow very slowly, in fact in some species it is not

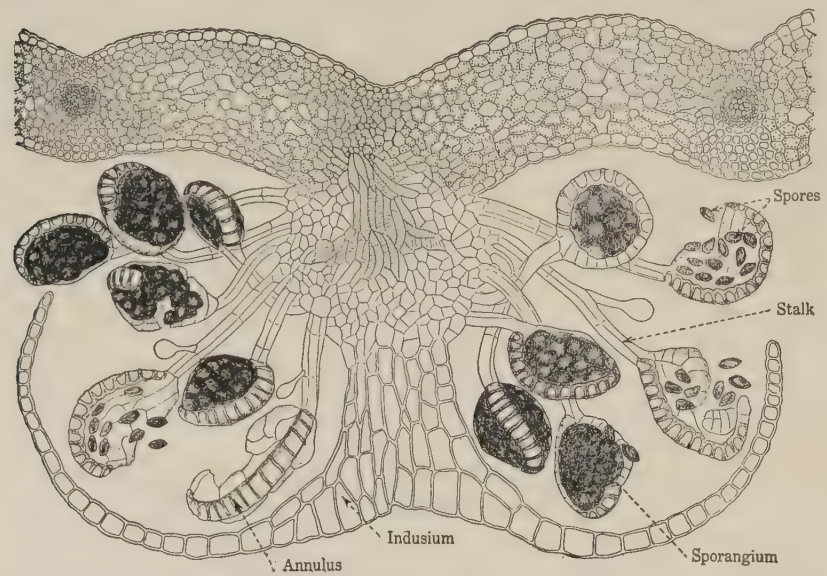


FIG. 353.—Cross section of fern leaf, through a sorus. Note the epidermal layers, chlorenchyma and veins of the leaf, as in higher plants. Different views of the sporangia are shown. (Redrawn from Kny.)

until the spring of the third year following their origin that the leaves appear above the ground.

Fern leaves continue to grow at the apex until their full size is reached. In this particular they differ from the leaves of seed plants, in which growth is apical only in very young leaves. They are of much the same structure as those of seed plants, having an upper and lower epidermis, chlorenchyma tissue, vascular bundles, and stomata. The stomata are usually confined to the under surface. The chlorenchyma is generally not sharply differentiated into palisade and spongy parenchyma.

The Sporangia.—The sporangia of *Polypodium* grow in groups on the under side of the leaves, which are accordingly often spoken of

as **sporophylls.** They form small, brownish groups called **sori** (singular **sorus**).

In *Polypodium* all the fronds are sporophylls; that is to say, the functions of photosynthesis and spore production are combined in all the leaves and there is no differentiation into sporophylls and vegetative leaves.

In *Polypodium*, and other leptosporangiate ferns, each sporangium consists of a **stalk** and a **capsule.** The wall of the capsule is composed of a single layer of thin-walled cells except for the **annulus,** a row of cells extending from the stalk over the top of the capsule and part way down

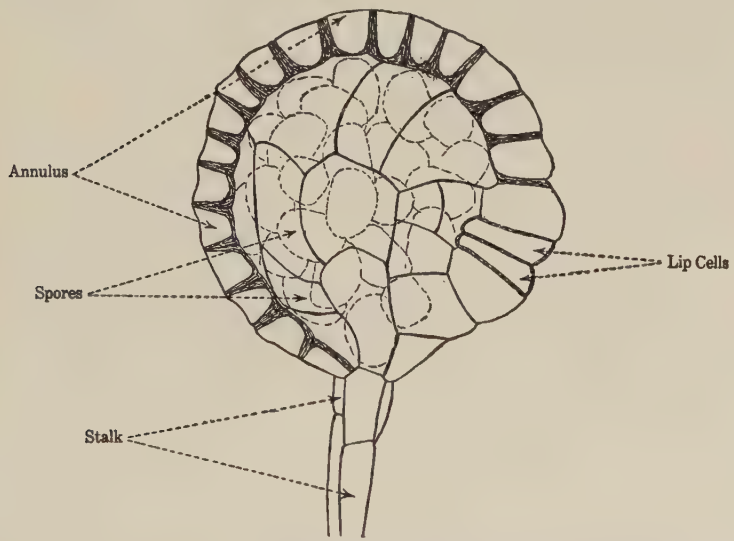


FIG. 354.—Surface view of a sporangium of *Polypodium*, before dehiscence. The spores within the capsule can be seen through the transparent wall which consists of a single layer of thin-walled cells. (Adapted from drawing by D. H. Campbell.)

the other side. The inner and radial walls of the cells composing the annulus are much thickened, while the outer walls are relatively thin. This structural arrangement is of importance as will be seen when the opening of the sporangium is described. Between the end of the annulus and the stalk are a few thin-walled cells, two of which, the **lip cells,** are narrow and radially elongated. At maturity the sporangium wall splits between these two-lip cells.

In *Polypodium*, and in all other leptosporangiate ferns, the sporangium originates from a single epidermal cell. By repeated division of this cell, the sporangium is developed. Besides the single-layered

wall there is a tapetum of one or two layers of cells, and a central mass of sporogenous tissue. The sporogenous tissue of each sporangium becomes organized into a number (usually sixteen) of large cells, rich in

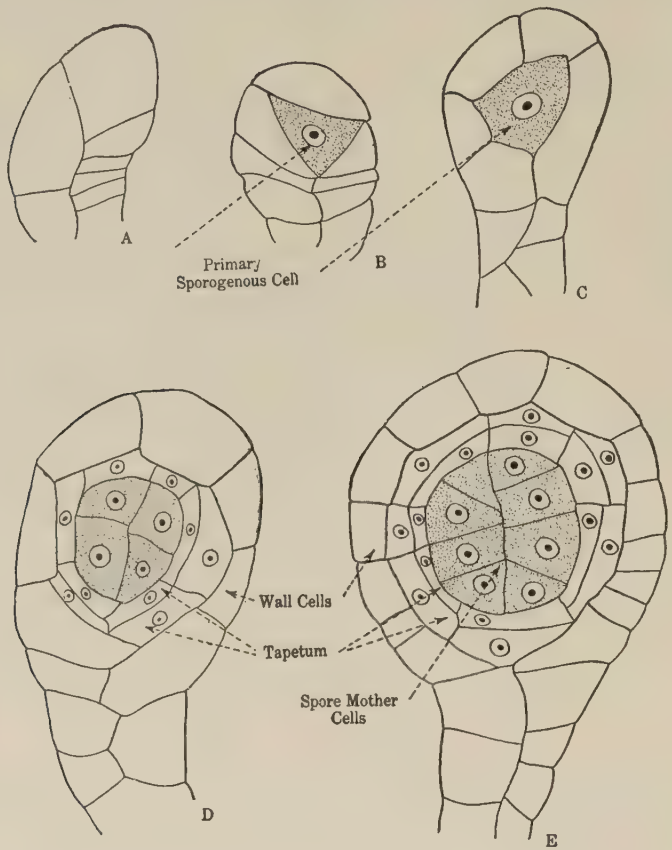


FIG. 355.—A series of stages in the development of the sporangium of *Polypodium*. *A*, just before the formation of the wall which cuts off (as shown in *B*) the primary sporogenous cell from the other cells of the young sporangium. *C*, a somewhat later stage; two of the cells surrounding the primary sporogenous cell have divided. *D*, tapetal cells have been cut off from the primary sporogenous cell and some of these tapetal cells have divided tangentially; within the tapetal layer four cells have been formed which will divide further to form spore mother cells as shown in *E*. (*D* and *E*, drawn from microtome sections prepared by D. H. Campbell.)

protoplasm, the spore mother cells. By two successive divisions, the first of which is a reduction division, each spore mother cell forms a tetrad of spores.

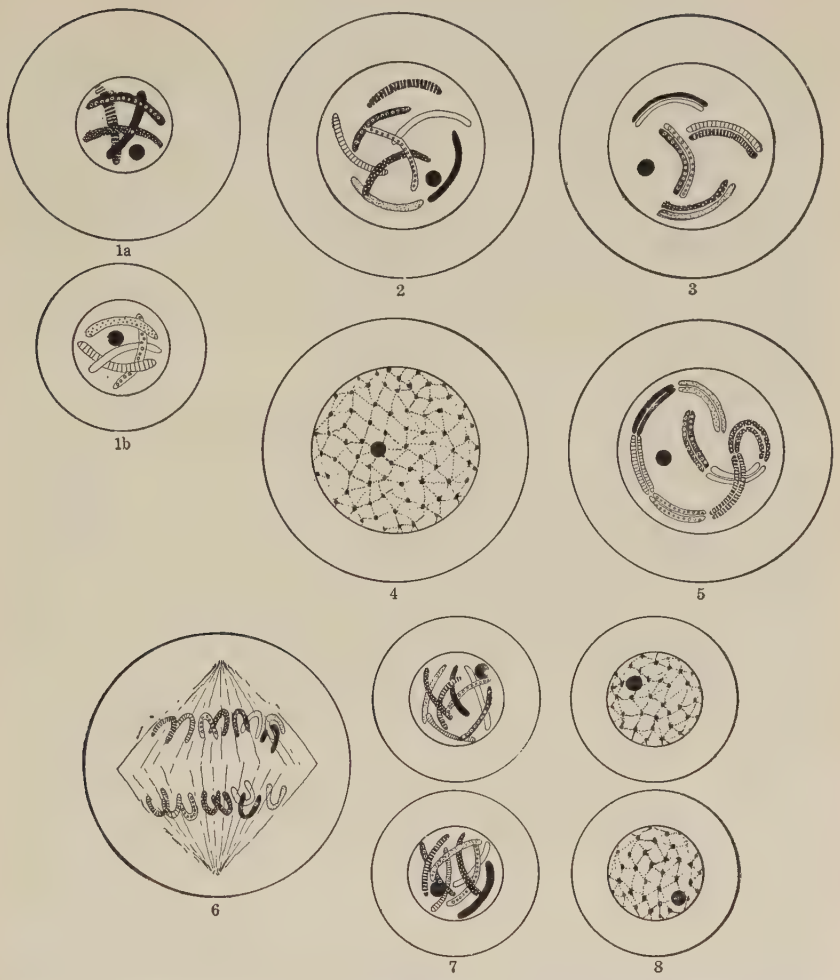


FIG. 356.—Diagrams showing chromosome behavior at the union of gametes and also in the mitosis of the zygote and all ordinary cell divisions of the sporophyte. In the diagrams the maternal chromosomes are black, the paternal chromosomes white. The homologous chromosomes have similar markings. The haploid number of chromosomes is four. 1*a* and 1*b*, female and male gametes respectively. 2, zygote resulting from union of 1*a* and 1*b*; note that the chromosome number has been doubled. 3, the chromosomes contributing the male and female gametes respectively maintain their identity. 4, zygote in the resting stage. 5, prophase in the process of cell division of the zygote; the spireme has segmented into the diploid number of double chromosomes. 6, anaphase. 7, first stage in the reorganization of daughter resting nuclei; note that the daughter nuclei have received one-half of each chromosome and thus bear the same hereditary qualities. 8, daughter cells resulting from the first division of the zygote with nuclei in the resting stage. The gametic composition and chromosome number of each of these are similar to those in stage 2.

Soon after the formation of the spore mother cells, the walls of the tapetal cells break down and the spore mother cells come to float in the tapetal protoplasm in the cavity of the sporangium. The spore mother cells and later the young spores absorb food from the tapetal protoplasm.

Reduction Division.—Reduction in the number of chromosomes takes place during the first of the two successive divisions of the spore mother cell which result in the formation of a tetrad of spores. Thus, the spore mother cells have diploid nuclei and belong to the sporophyte generation, whereas the spores have haploid nuclei and belong to the gametophyte generation.

In the chapter on The Cell, the ordinary process of cell division was described in some detail. In that description it was shown how in the division of the nucleus, the two daughter nuclei each receive an equal amount of chromatin, and how each of these daughter nuclei has a number of chromosomes equal to that of the mother cells. Thus in an ordinary mitosis there is no reduction in the number of chromosomes. It will be recalled that in all plants having sexual reproduction a reduction division takes place somewhere in the life cycle. We shall now describe the reduction division of a spore mother cell of *Polypodium*. This is a continuous process which it is, however, convenient for purposes of discussion to divide into the following stages:

1. *The chromatin of the resting nucleus of the spore mother cell is evenly distributed. At the beginning of the nuclear division, this chromatin becomes arranged in the form of a thread, which consists of two parallel strands.* There is reason to believe that the chromatin material of one of the strands is derived from the sperm, and that of the other strand from the egg which fused to form the zygote from which the sporophyte developed. It should be pointed out here that in all the successive divisions of the zygote resulting in the multicellular sporophyte, the chromosomes contributed by the male gamete (paternal chromosomes) and by the female gamete (maternal chromosomes) maintain their individuality in the nuclei of sporophyte cells. It is, however, only at the time of reduction division that the separate identity of the maternal and paternal chromatin becomes apparent.

2. *The paired threads of chromatin contract and then unite along their entire length. There is a characteristic knotting of the chromatin threads.* There is evidence that during the close union of the paired threads an interchange of chromatin may take place between maternal and paternal chromosomes.

3. *The two threads again become distinct, and then divide transversely into a definite number of paired chromosomes* (5 in Fig. 357). The

FIG. 357.—Diagrams showing chromosome behavior during the reduction division of a spore mother cell of *Polypodium*, and the subsequent division resulting in the formation of spores. In the diagrams the maternal chromosomes are black, the paternal white, and homologous chromosomes have similar markings. 1, Resting nucleus of the spore mother cell. 2, The chromatin has become arranged in

Continuation of the legend on the next page.

number of pairs of chromosomes is seen to be one-half the diploid number.

4. *The chromosomes of each pair are somewhat twisted about each other and each member splits lengthwise* (not shown in diagram but double nature of each member of pair is shown in 6).

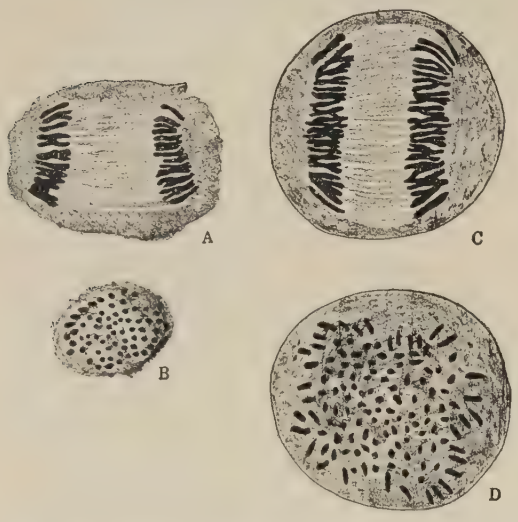


Fig. 358.—Nuclei of the gametophyte (*A* and *B*) and of the sporophyte (*C* and *D*), of *Nephrodium*, showing 64 and 128 chromosomes respectively. (Redrawn from Yamanouchi.)

5. *At about this time the spindle is formed and the nucleoli and nuclear membrane disappear. One member of each pair of chromosomes moves toward one pole, and the other member of the pair toward the opposite pole.* (6 and 7 of Fig. 357.) Thus each daughter nucleus has one-half the diploid number of chromosomes and each one of the daughter nuclei receives either a paternal or a maternal chromosome from each pair. However, it is only by chance that the chromosomes of a daughter nucleus are all paternal or all maternal. Each of the chromosomes after the separation of the members of a pair is itself double in nature.

the form of a thread, consisting of two parallel strands. The chromatin material of one strand is derived from the male gamete and that of the other strand from the female gamete. 3 and 4, The paired threads of chromatin have contracted and become twisted about each other. 5, The paired thread breaks up transversely into the haploid number of chromosomes. Each chromosome is seen to be made up of homologous maternal and paternal characters. 6 and 7, One member of each pair of chromosomes moves toward one pole, and the other member of the pair toward the opposite pole, and each member splits lengthwise. Also note that each of the daughter nuclei receives either a paternal or a maternal chromosome from each pair. 8, The daughter nuclei resulting from the first division of the spore mother cell (1) each have one-half the number of chromosomes possessed by the spore mother cell. 9 and 10, Each daughter nucleus promptly undergoes a second mitosis, which is, however, of the ordinary type and does not involve any reduction in chromosome number. 11, Four spores derived, by two successive divisions, from the spore mother cell. The haploid nuclei are in the resting stage.

6. *Each daughter nucleus resulting from the first division of the mother cell promptly undergoes a second mitosis of the ordinary type, which does not involve any reduction in chromosome number, nor any separation of maternal from paternal chromosomes.*

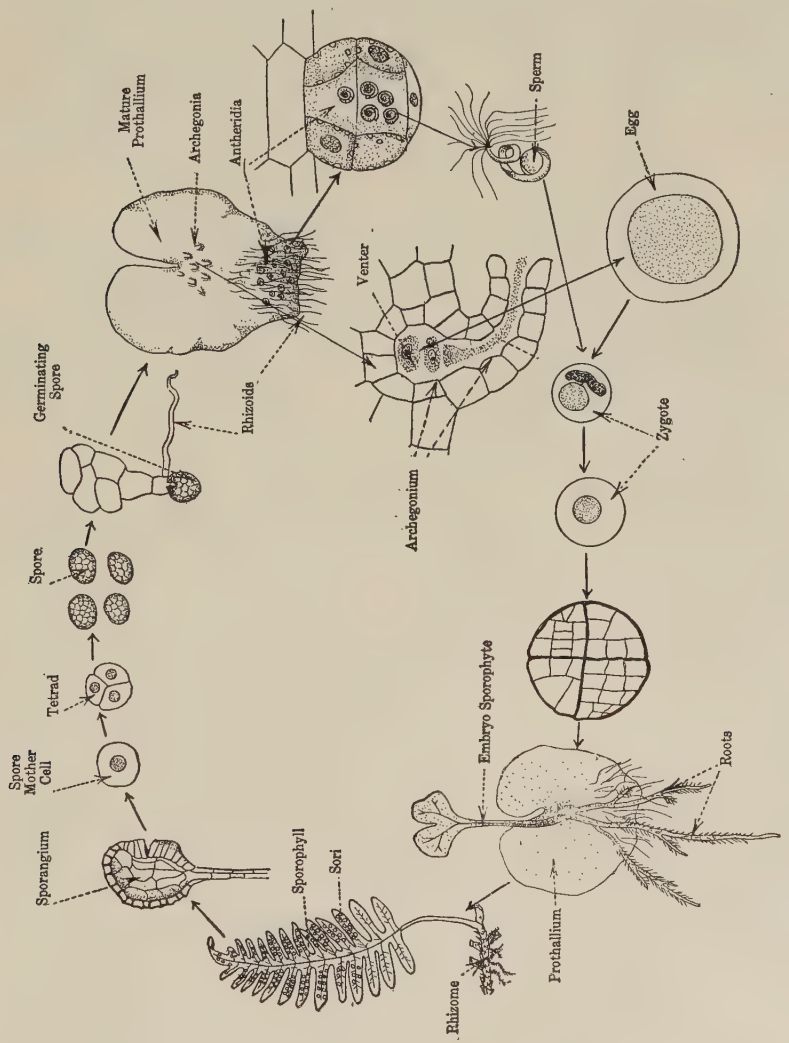


FIG. 359.—Diagrams showing stages in the life cycle of a true fern (*Polypodium*).

7. *Each of the four haploid nuclei thus formed, together with part of the cytoplasm, is surrounded by a wall and becomes a spore.*

Dehiscence.—As the sporangium becomes progressively drier, the annulus begins slowly to straighten out, and as it does so the weak lip

cells and the thin side walls of the sporangium are torn. Finally, the annulus may almost double back upon itself, pulling with it a mass of ripe spores. Suddenly, with a snap, the annulus returns to its original position, at the same time dispersing the spores. In their dry condition the spores are easily disseminated by wind.

Summary of Life Cycle.—The life history of *Polypodium* may be summarized as follows:

1. The spores, which have the haploid number of chromosomes, are discharged from the sporangia, which are borne in clusters on the under surface of the sporophyll.

FIG. 360.—Habit sketch of *Marsilia quadrifolia*. Note the oval sporocarps. (After Wettstein.)

2. Under proper conditions of moisture and temperature, the spores germinate, each producing a short green filament.

3. By a series of divisions of an apical cell, the green filament grows into a flat, heart-shaped structure, the *prothallium* (gametophyte) which is attached to the soil by numerous rhizoids.

4. Gametangia are borne on the ventral surface of the prothallium. In *Polypodium*, antheridia and archegonia occur on the same prothallium.

5. Each antheridium usually produces thirty-two multiciliate-sperms, and each archegonium develops a single egg-cell.

6. Fertilization of the egg cell takes place in the venter of the archegonium. At fertilization the chromosomes of the haploid egg and sperm nuclei are united in the zygote nucleus, which has, therefore, the diploid number of chromosomes half maternal and half paternal. The zygote is thus the beginning of the sporophyte generation.

7. Successive divisions of the zygote result in the development of the embryo sporophyte, consisting of foot, root, primary leaf and stem. The foot is a temporary structure absorbing, during a short time only, food from the prothallium to which it is attached. The foot dies after the primary root and stem have developed to the point where they can supply sufficient water and food for the young sporophyte. And, after leaves and adventitious roots have developed on the stem, the primary leaves and roots also die, so that only one of the four primary

organs (the stem) is permanent. The mature sporophyte consists of a rhizome, bearing roots and fronds. On the under side of the fronds, sporangia are borne in clusters called **sori.**

8. The sporogenous tissue of each sporangium forms, in *Polypodium,* sixteen spore mother cells. Each of these, by two successive divisions, the first of which is a reduction division, gives rise to four spores with haploid nuclei. At the reduction division the maternal and paternal chromosomes of any pair are separated from each other and pass to different daughter cells.

FIG. 361.—*Azolla* plant magnified about eight times.

FIG. 362.—Habit sketch of *Salvinia Natans.* (After Wettstein.)

The relation of *Polypodium,* the fern we have selected as a type, to other true ferns is shown in the following brief classification:

Class Filicineae

Sub-class 1. *Eusporangiate* ferns. All homosporous and already mentioned on page 490.

Sub-class 2. *Leptosporangiate* ferns.

(*a*) Homosporous—*Polypodium* and all other common ferns.

(*b*) Heterosporous—The **water ferns,** including the genera *Salvinia, Azolla, Marsilea,* and *Pilularia.* In these, two kinds of spores are produced, small spores (**microspores**) and large spores (**megaspores**) which give rise respectively to male prothallia and female prothallia.

In *Polypodium,* as in most common ferns, it will be recalled that all fronds are similar and may produce sporangia. In such ferns as the cinnamon fern (*Osmunda cinnamonea*), the sensitive fern (*Onoclea sensibilis*), and others, there are, however, two sorts of leaves, sterile and fertile. The former are green, expanded leaves of ordinary foliage

type and never produce sporangia. The fertile leaves are much smaller, their cells contain very little chlorophyll, and they may be completely covered with sporangia.

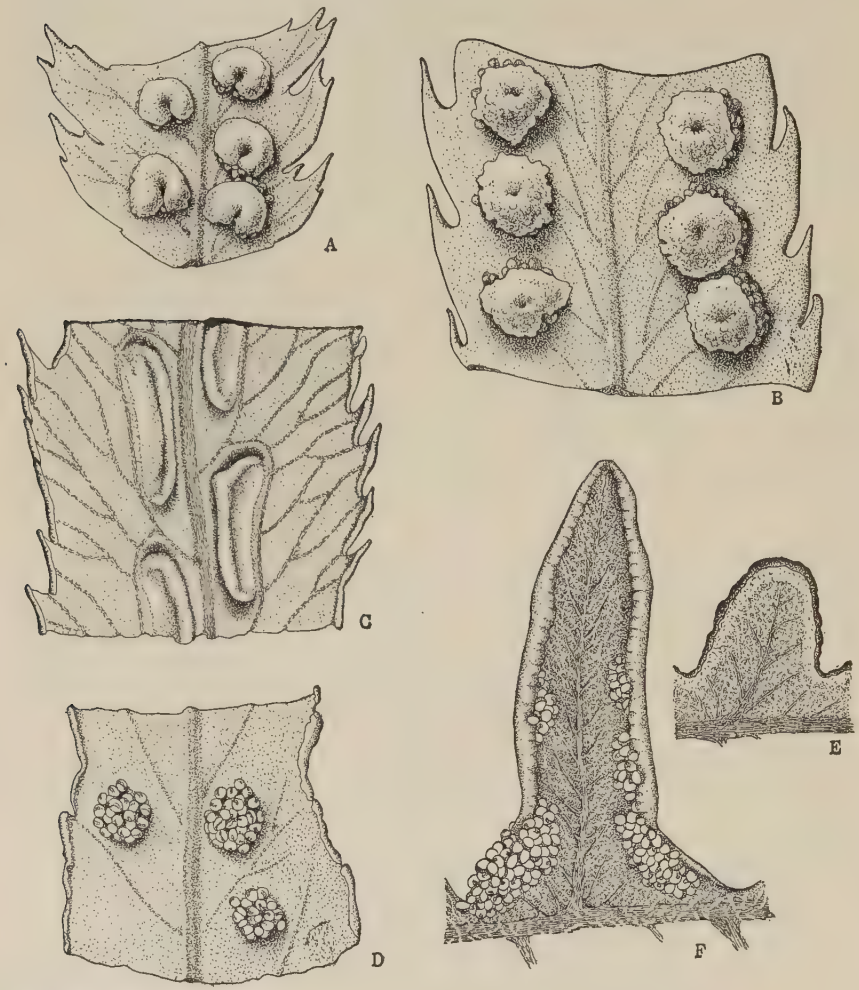


FIG. 363.—Sori and indusia of various types. *A*, sori of *Dryopteris* with kidney-shaped indusia. *B*, shield-shaped indusia of *Polystichum* sori. *C*, linear indusia covering the sunken sori of *Woodwardia*. *D*, naked sori of *Polypodium* which are without indusia. *E*, and *F*, a young and an older pinnule of *Pteris* showing the false indusium (inrolled margin of the leaf) characteristic of *Pteris* and several related genera.

In many ferns, the sori are covered by a membranous outgrowth of the epidermis, known as an **indusium.** The form and arrangement of sori and indusia are characters which are much used in the classi-

fication of ferns. In *Polypodium* and many other genera, indusia are absent, and the sori are said to be **naked.** A so-called " false indusium," formed by a folding over of the margin of the frond so as to cover the sporangia, occurs in the common bracken (*Pteris aquilina*) and in related ferns such as the maiden-hair fern (*Adiantum*).

The heterosporous ferns are a group of aquatic or amphibious forms known as the " water ferns." They differ from *Polypodium* and other common ferns in the production of two kinds of spores, small (microspores) and large (megaspores) which give rise to male prothallia and female prothallia respectively. The microsporangia and megasporangia are borne in characteristic spherical or oval bodies known as **sporocarps.** The sporangia resemble in general structure those of *Polypodium,* which we have described, except that they have no annulus. In water ferns, the gametophytes are short-lived and greatly reduced structures. They do not possess chlorophyll, their food supply being restricted to that furnished to the developing spores by the sporophyte. The gametophytes are therefore entirely dependent upon the sporophyte generation. In the extreme reduction and complete dependence of the gametophyte generation they closely resemble the heterosporous genus *Selaginella,* which will later be described.

EQUISETINEAE (THE HORSETAILS)

General Characteristics.—The second class of the Pteridophyta, the Equisetineae or Horsetails, is represented among living plants by only a single genus, *Equisetum,* of which there are about thirty species. That the Equisetineae were formerly a much more important element in the flora of the earth than they are to-day is shown by the considerable number and variety of such plants of which fossil remains have been found. The fossil Equisetineae include species of the genus *Equisetum* which greatly exceeded the living species in size and which were tree-like in form. In addition there are fossil remains of several other genera including the genus *Calamites.* Some of the latter plants were heterosporous, that is they produced, like the water ferns already mentioned and *Selaginella* which we shall later discuss, two kinds of spores, microspores and megaspores, which gave rise respectively to male and female gametophytes.

The living equisetums vary greatly in size; for example, the South American species, *Equisetum giganteum,* may grow to a height of thirty feet though its stem diameter is only a few centimeters, whereas certain species, like *Equisetum scirpiodes,* seldom exceed 20 centimeters in height.

In the Equisetineae as in the Filicineae, the sporophyte is the conspicuous generation. It is made up of a branched system of horizontal

underground rhizomes from which, each season, erect aerial shoots are sent up. The most striking characteristics of the sporophyte plant are:

1. The heavy impregnation of the outer tissue with silica
2. The reduced scale-like leaves
3. The distinct hollow internodes of the aerial stems.

FIG. 364.—The sporophyte of common horsetail (*Equisetum arvense*), showing green vegetative shoots (*a*) and spore-bearing shoots (*b*). The aerial shoots arise from the rhizome (*r*) with tuberous storage organs; *l*, scale leaves; *sp*, sporangium. (After Curtis.)

The siliceous deposit gives to the shoots a harsh texture, and on this account the plant was formerly used for cleaning and polishing metal utensils and given the name of "scouring rush." On account of the reduced size of the leaves, photosynthesis is carried on principally by the stems.

The horsetails grow for the most part in moist locations and are fre-

quently found as weeds in poorly drained agricultural land. Hay containing considerable quantities of *Equisetum* is known to be injurious to livestock.

Other characteristics of the Equisetineae besides those mentioned and which distinguish them from the Filicineae are the peculiar form of the sporophylls and the grouping of these at the tip of the aerial shoots into cone-like structures called **strobili** (singular **strobilus**).

The commonest species, *Equisetum arvense*, is very widely distributed throughout the northern hemisphere. We shall use it as a type of the group and briefly describe its life history.

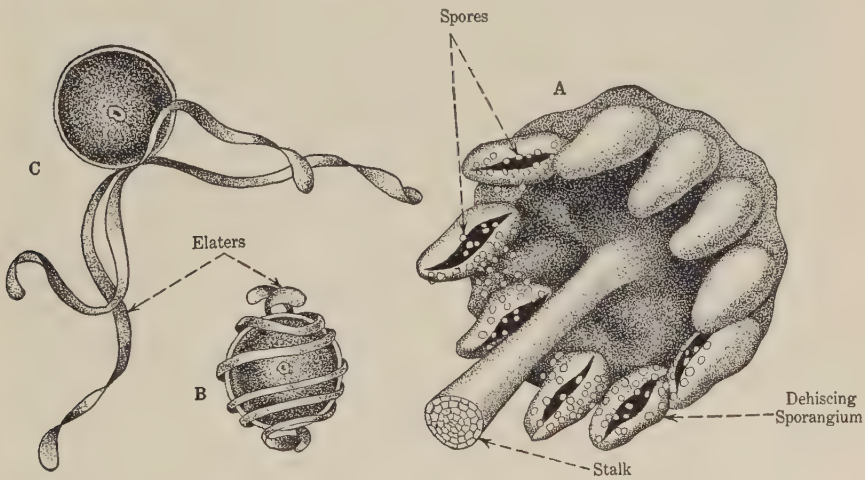


Fig. 365.—Equisetum. *A*, ventral view of a sporophyll. *B*, mature spore with elaters coiled about the spore body. *C*, spore with elaters uncoiled. (Redrawn from Wettstein, after Dodel-Port.)

Life History of Equisetum-Gametophyte.—The asexual spores are all morphologically alike, that is, the plant is homosporous. The spores are globular and green in color. In addition to the usual two intine and exine wall layers there is developed outside of the exine a third layer called the **perinium.** In the mature spore, the perinium ruptures, forming four ribbon-like appendages (**elaters**) which coil around the spore body. These elaters are very sensitive to changes in atmospheric humidity; when the air is dry, they uncoil; when it is humid, they again coil around the spore. In this movement, elaters of adjoining spores become entangled, and consequently the spores are carried away in groups. The spores are capable of immediate germination.

This species, and in fact all the species of *Equisetum*, are dioecious; that is, some of the spores produce male gametophytes which bear

antheridia only and others give rise to female or archegonial gametophytes, but there is no distinction between the spore in size or in form.

The gametophytes are small, green, irregularly lobed thalloid structures, the male gametophytes being one cell in thickness, while the female gametophytes are larger and more massive. The latter develop a relatively thick cushion of cells upon which the archegonia are borne.

The archegonia and antheridia of *Equisetum* are very similar to those of the ferns, although somewhat more reduced, and the sperms are multiciliate as in the Filicineae.

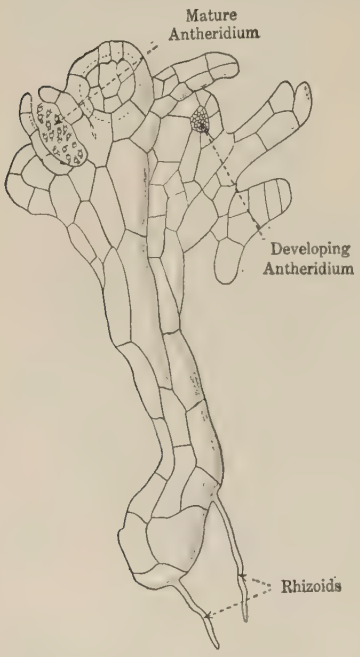


FIG. 366.—*Equisetum*. Mature male gametophyte. (Redrawn from Hofmeister.)

Liberation of the sperms and fertilization take place much as in the true ferns and the development of the sporophyte from the zygote is much as in *Polypodium*. The sporophyte is dependent upon the gametophyte for a short period only.

The Sporophyte.—The mature sporophyte consists of a perennial rhizome from which roots and aerial shoots are produced. The aerial stems have a rough surface and their division into nodes and internodes is very distinct. The internodes are hollow and are marked with a number of longitudinal grooves. At each node there is a whorl of small, pointed structures, the very much reduced foliage leaves, which are joined at their bases, forming a sheath around the stem.

In *Equisetum arvense* there are two kinds of aerial shoots: reproductive and vegetative. In the early spring there are sent up from the rhizomes, simple, unbranched reproductive shoots, each of which bears at the tip a single, terminal, cone-shaped, whitish group of sporophylls (strobilus). These spore-bearing shoots die down soon after spore production, and are succeeded by slender, four-cornered, green, sterile shoots which send out numerous branches in whorls at the nodes.

Strobilus and Sporangium.—The strobilus consists of an axis with much shortened internodes. At the nodes there arise shield-shaped structures (sporophylls) which bear sporangia. Hence, the strobilus is a specialized part of a shoot beset with sporophylls. It should be stated

in this connection that the flower of the higher plants is also an axis which bears sporophylls.

The sporangia are long sacs on the under side of the sporophyll, and since each arises from a single epidermal cell they are of the leptospo-

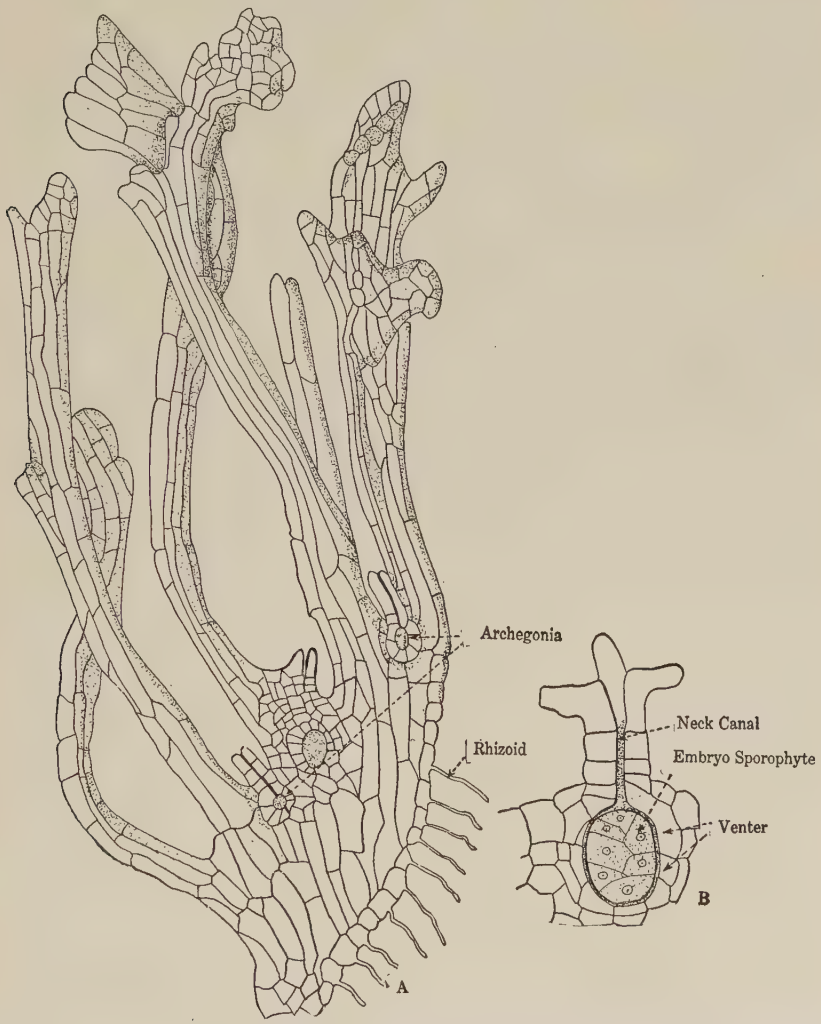


FIG. 367.—*Equisetum*. *A*, female gametophyte. *B*, embryo sporophyte in venter of archegonium. (*A*, redrawn from Hofmeister. *B*, redrawn from Sadebeck.)

rangiate type. There is a tapetum consisting of two or three layers of cells. Each sporophyll bears five to ten sporangia. At maturity the sporangia dehisce longitudinally, and the spores fall out.

There are a number of points in this life history of *Equisetum* worthy of special emphasis: (1) The sporangia are produced on specialized sporophylls. (2) The spores are similar as in the majority of true ferns, but certain extinct forms related to *Equisetum* were heterosporous.

LYCOPODINEAE (THE CLUB MOSSES)

General Characteristics.—The Lycopodineae, like the Equisetineae, constitute a class which was formerly represented by much larger, more numerous, and more highly differentiated species than exist to-day. The number of species of living Lycopodineae greatly exceeds, however, the living species belonging to the Equisetineae, the two common genera *Lycopodium* and *Selaginella* including nearly six hundred species.

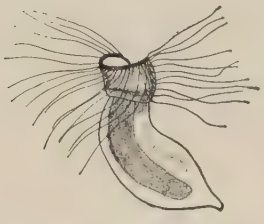


FIG. 368.—Sperm of *Equisetum*. (Redrawn from Belajeff.)

Remains of certain fossil representatives of this class are abundant in the coal beds. Among the most interesting of these fossil relatives of the modern club mosses are the arborescent genera, *Lepidodendron* and *Sigillaria*. Fossil *Lepidodendron* trunks having a length of over 30 meters have been found. Some of the extinct Lycopodineae had stems in which secondary growth in thickness took place through the activity of a cambium, much as in present-day gymnosperms and dicotyledons. The structure of their leaves and stems was much more complicated than in the case of the living species of the Lycopodineae.

Most of the species of *Lycopodium* and *Selaginella* are found growing as terrestrial plants or as epiphytes in moist tropical forests, but they do not constitute an important element in the flora of the temperate and colder parts of the earth.

The Lycopodineae differ from the Filicineae and the Equisetineae principally in that:

1. The sperms are biciliate instead of multiciliate;

2. The sporophylls, though resembling the vegatative leaves as in most of the true ferns, are grouped in strobili as in *Equisetum*; and

3. There occurs in the life cycle a temporary sporophyte organ (the **suspensor**), lacking in other pteridophytes but found in the seed-bearing plants.

Selaginella is an excellent type for the study of a pteridophyte showing an approach to the seed plants in having well-marked heterospory, and a very greatly reduced gametophyte, even though it appears to be in

some respects a much more primitive form than the true ferns. On account of the much reduced character of the gametophytes, which are not visible to the naked eye, we shall begin our account of the life history of *Selaginella* with the sporophyte, which as in all the Pteridophyta is the more conspicuous generation.

Life History of Selaginella. The Sporophyte.—In the creeping species of *Selaginella* the shoot is dorsiventral, the leaves are small and arranged on the axis in four longitudinal rows. Certain structures arising from the leafy stems and known as "rhizophores," although not roots, act as supporting structures and give rise to roots when they come into contact with the soil. The leaves have a loose, spongy mesophyll, and a well-developed epidermis with stomata which are usually confined to the under surface. The chloroplasts are large and few in number, and in some species there is only one in each cell.

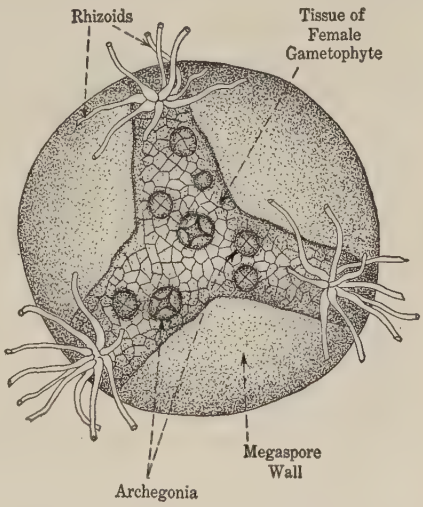


FIG. 369.—Megaspore of Selaginella, containing mature female gametophyte, as seen from the upper side. The wall of the megaspore has been burst by the enlarging female gametophyte which is seen protruding. (Redrawn from Bruckmann.)

Strobilus and Sporangia.—The strobili (cone-like groups of sporophylls) are lateral branches on which the leaf-like sporophylls are borne, generally in four rows so that a rather compact four-angled or club-shaped structure is formed.

Attention has already been called to the fact that *Selaginella* is heterosporous, like the water ferns which were mentioned earlier in this chapter. Heterospory, which is the habit of producing small spores which give rise to male gametophytes and larger spores from which the female gametophytes develop, was characteristic of many of the extinct pteridophytes. Although it is not common among living ferns and fern allies, it is universal among the spermatophytes or seed-bearing plants.

Corresponding with the difference between the two kinds of spores (**microspores** and **megaspores**) of heterosporous plants are differences in the sporangia (**micro-** and **megasporangia**) and in the

sporophylls upon which the sporangia are borne (**micro-** and **megasporphoylls**).

The strobili of *Selaginella* are bisporangiate in that they are made up of both microsporophylls and megasporophylls. The groups of sporophylls (cones or strobili) of the gymnosperms are, on the other hand, monosporangiate, so that there are megasporangiate and microsporangiate cones. In the angiosperms, however, microsporophylls (stamens) and megasporophylls (carpels) are generally found together in the same group (flower).

In *Selaginella* each of the megasporophylls bears a single megasporangium within which four large spores (the megaspores) are produced. The microsporophylls also bear solitary sporangia (microsporangia), within which, however, numerous (generally sixty-four) spores (microspores) are produced.

Development of Spores.—Up to formation of the spore mother cells the development of the microsporangia and megasporangia is the same, and not essentially different from that of the sporangia of true ferns. Each sporangium consists of a short stalk and an enlarged portion within which the spores are produced. The wall of the sporangium consists of three layers of cells, of which the innermost is a tapetal layer similar to that found in the true ferns (Filicineae) and in *Equisetum*. The same number of spore mother cells (usually sixteen) are generally formed in both the micro- and megasporangia.

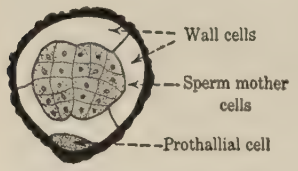


Fig. 370.—Male gametophyte of *Selaginella*.

Each microspore mother cell gives rise to four spores, so that sixty-four spores are generally produced in each microsporangium. The first division of the functioning spore mother nuclei in both microsporangia and megasporangia is a reduction division and marks the end of the sporophyte and the beginning of the gametophyte generation.

However, in most species of *Selaginella*, only one of the spore mother cells in the megasporangium divides; accordingly the number of megaspores is four in most species. The other spore mother cells undergo disorganization and their protoplasm furnishes food for the developing spores which are accordingly better nourished than are those of the microsporangium and are able to attain a very much larger size.

The Male Gametophyte.—The microspores begin to germinate before they are shed from the microsporangium. This is in marked contrast with conditions in other pteridophytes which we have studied, but we shall see that in all the Spermatophyta the germination of the

microspores is initiated before their release from the sporangium. The male gametophyte of *Selaginella* is formed entirely within the microspore. After the division of the nucleus of the microspore, at the time of its germination, a wall is formed which divides the spores into two cells of very unequal size. The spores are usually shed in this two-celled condition. Subsequently, the larger cell of the two goes through a series of divisions which result in the formation of a central group of cells, and a single layer of wall cells. The protoplast of each cell of the central group develops into a single sperm. The smaller cell of the first two formed (i.e., the **prothallial cell**) is considered to be homologous with the vegetative cells which make up the greater part of the fern prothallium. All the rest of the gametophyte is believed to represent a single antheridium. The prothallial cell is merely a vestigial structure; it does not possess chlorophyll, and probably plays no essential part in the life history of the plant. The gametophyte is unable to carry on photosynthesis and is entirely dependent upon the sporophyte. This is just the reverse of the condition existing in most liverworts where the sporophyte is completely dependent upon the gametophyte.

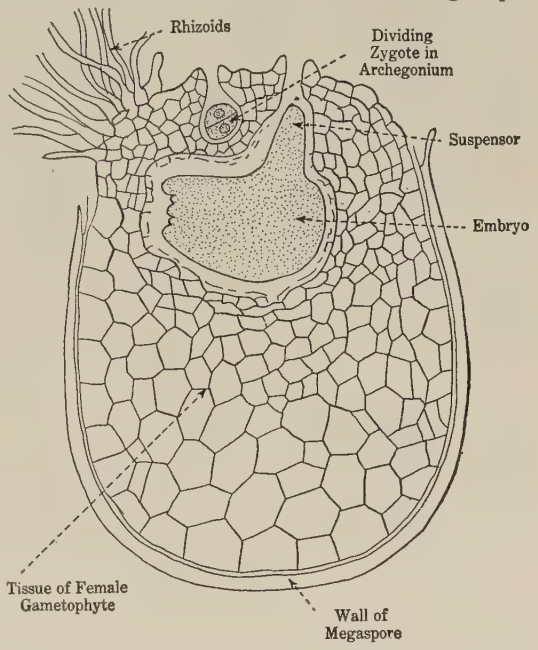


FIG. 371.—Longitudinal section of female gametophyte of *Selaginella*, protruding from the ruptured megaspore. (Redrawn from Bruckman.)

The Female Gametophyte.—Germination of the megaspores which generally commences before they are shed from the megasporangium, begins by the division of the single megaspore nucleus into two nuclei, between which no wall is formed. By continued free division of the nuclei, there are formed within the megaspore a large number of nuclei most of which accumulate at one end of the spore. The walls are formed simultaneously between the nuclei and thus a mass of tissue (the female

gametophyte) is formed within the megaspore. By growth of the gametophyte the megaspore wall is finally ruptured and gametophytic tissue is exposed. Several archegonia develop upon this exposed surface. In some species rhizoids which do not function, are produced from the exposed tissue and there may be some development of chlorophyll in this region.

The archegonia do not differ from those of the true ferns and *Equisetum* in any important particular. Each consists of a venter containing the egg, a single ventral-canal cell, a single neck-canal cell and a neck, composed of two tiers of four cells each. All this development of the female gametophytes takes place, at least in many species, while they are still within the megasporangium which remains attached to a megasporophyll of the strobilus.

Transfer of Microspores and Fertilization.—It will be recalled that the male gametophyte is enclosed by the microspore wall at the time when the microspores are shed, and further that the microsporophylls are generally situated above the megasporophylls on the strobilus. In some species of *Selaginella* the microspores when shed sift down between the megasporophylls and come to lie very near the megasporangia. If the plant is wet about this time by rain or heavy dew, the wall separating the sperms breaks down, the contents of the microspore swell, the microspore wall is ruptured and the biciliate sperms are set free. Previous to this time, the megasporangium wall has cracked open but not sufficiently to allow the female gametophytes to escape. The sperms swim to the archegonia, which are by this time ready for fertilization. It should be emphasized here that the presence of water is essential in order that the sperms may reach the archegonia, a condition which gives indication of the origin of *Selaginella* from aquatic ancestors.

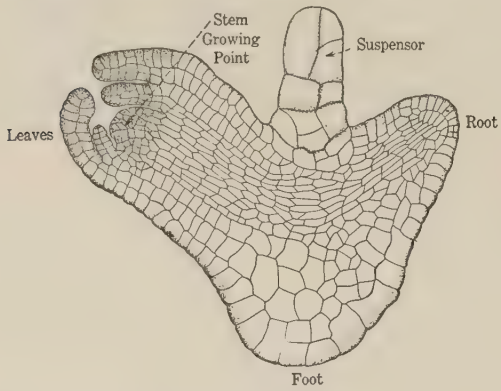


Fig. 372.—Embryo of Selaginella. (Redrawn from Bruckmann.)

The fertilized egg is the beginning of the sporophyte or diploid generation, and generally starts at once its development into an embryo sporophyte. The first division of the egg is by a transverse wall and

results in the formation of an outer cell known as the **suspensor cell**, and an inner cell, the **embryo cell** from which the embryo proper develops. The suspensor cell greatly elongates, pushing the developing embryo down into the deeper tissue of the female gametophyte, from which nourishment is absorbed. The suspensor cell may divide several times, but it takes no part in embryo formation. The suspensor is a structure which distinguishes the Lycopodineae from other Pteridophyta, but which occurs in practically all seed-bearing plants. The young embryo, embedded in the tissues of the female gametophyte and still enclosed within the megaspore wall, consists of a foot, a rudimentary root, and a rudimentary stem with two cotyledons. In some species the megaspores are not shed until after the growing stem and root of the embryo have begun to emerge from the female gametophyte or have even forced their way out through the sporangium wall.

After the female gametophytes are shed from the strobilus, the root soon enters the ground, the stem elongates, leaves are developed, and the young sporophyte becomes independent. The suspensor and foot are temporary structures.

Summary of the Life History of Selaginella.—

1. Germination of microspores, the initial stages taking place within the sporangium. Shedding of microspores with enclosed two-celled male gametophyte.

2. Further development of male gametophyte, which at maturity consists of a single prothallial cell and a central group of antheridial cells, each cell of which gives rise to a single sperm, and a single layer of wall cells surrounding the central group.

3. Rupture of microspore wall and liberation of biciliate sperms.

4. Germination of each megaspore within the sporangium to form a female gametophyte, which by its growth ruptures the spore wall at one side. At maturity the female gametophyte consists of a mass of small cells at the exposed end which develop archegonia, and a group of large cells at the opposite end. Early in the formation of the female gametophyte the nuclei multiply by free nuclear division, a condition which is also characteristic of all of the Spermatophyta.

5. Swimming of some of the sperms, if water is present, to the archegonia, and fertilization of the egg, followed by the formation of a cell wall about the zygote. The zygote is the beginning of the diploid phase.

6. Formation from the zygote, and within the female gametophyte tissue and megaspore wall, of a suspensor and an embryo consisting of foot, root, and stem with two cotyledons.

7. Further development of the sporophyte, during which the root enters the ground, the stem grows longer, and leaves and peculiar

leafless branches (rhizophores) forming roots at their ends are produced.

8. Formation, after a vegetative period, of strobili bearing both mega- and microsporophylls.

9. Development of microsporangia on microsporophylls, which usually occur near the apex of the strobili, and of megasporangia on megasporophylls, which usually occur near the base of the strobili.

10. Formation of four microspores by two successive divisions from each spore mother cell in the microsporangium. During the first division, the chromosome number is reduced, this reduction and the similar reduction during the formation of megaspores marking the end of the diploid phase.

11. Formation of four megaspores, by two successive divisions, from only one spore mother cell of the many in the megasporangium, the remaining spore mother cells disorganizing and furnishing nourishment for the single tetrad of spores.

Significant Points in the Life History of Selaginella.—Some of the most significant facts relative to *Selaginella* are:

1. The production of two kinds of spores (heterospory)—microspores and megaspores.

2. The grouping of the sporophylls in a strobilus.

3. The extreme reduction of the male and female gametophytes, which are completely dependent on the sporophyte, most marked in the male gametophyte which consists of a single antheridium and one vegetative cell.

4. Retention of the spores and contained gametophyes within the sporangia until their development is far advanced.

5. Development of the new sporophyte from one of the two cells resulting from the first division of the zygote. From the upper cell there is developed a new structure called the suspensor, which is also found in the seed plants.

6. Dependence of the gametophytes upon the sporophyte which is just the reverse of the condition existing in mosses and liverworts where the gametophyte is the independent generation and the sporophyte is totally or partially dependent upon it.

Lycopodium.—As was previously stated, the two most common genera of the class Lycopodineae are *Selaginella* and the homosporous genus, *Lycopodium*. In *Lycopodium*, the stem branches extensively, the leaves are small, and are arranged spirally on the stem. Another and more important distinction between these two genera is that *Lycopodium* is homosporous, whereas *Selaginella* is heterosporous. In all *Lycopodium* species, the gametophytes are monoecious, while in *Selag-*

inella, as of course, in all heterosporous forms, they are dioecious. In some species of *Lycopodium* the gametophytes are small, chlorophyll-free structures, which live saprophytically under ground, but in other species they are green and develop on the surface of the soil. In no case are they dependent on the sporophyte.

SUMMARY OF THE PTERIDOPHYTA

1. Alternation of generations is well developed in all Pteridophyta.

2. In all of them the sporophyte possesses a root and thus frees itself early from all dependence upon the gametophyte.

3. In addition, the sporophyte possesses leaves, organs which never occur upon the sporophyte of the Bryophyla.

4. Spores are produced not in a single terminal capsule, but in many sporangia borne on sporophylls.

5. Because the sporophyte of ferns and their allies is better adapted to life on land than the gametophyte of liverworts and mosses, the pteridophytes are larger and more successful plants than any bryophytes.

6. Heterospory first occurs in certain of the Pteridophyta. Both homosporous and heterosporous forms occur, however, in this division.

7. In the formation of spores in all Pteridophyta, the same essential change takes place as in spore formation in the Bryophyta, i.e., the development of a tetrad from each spore mother cell. This tetrad is the result of two successive divisions of the spore mother cell, and during the first of the two divisions the chromosomes are reduced to the haploid number.

8. As contrasted with the Bryophyta, the Pteridophyta show a marked reduction of sporogenous as compared to vegetative tissue.

9. In all ferns, as also in Bryophyta, the structure of the gametangia is essentially the same, as is also the method of fertilization.

10. Fertilization in all ferns is dependent, as in the Bryophyta, upon the presence of water.

11. In general, the gametophytes of the Pteridophyta are much smaller and simpler than those of the mosses and liverworts.

12. In some of the heterosporous Pteridophyta the female gametophyte and the young sporophyte are retained for some time within the sporangium, a step toward the seed-bearing habit.

13. In certain Pteridophyta—*Selaginella* and *Lycopodium*—a new structure, the suspensor, is developed from one of the first two cells formed from the zygote. The presence of this structure indicates relationship of such forms to the Spermatophyta, all of which have a suspensor.

CHAPTER XV

THE SPERMATOPHYTA

The fourth division of the Plant Kingdom, the Spermatophyta, by far exceeds in importance, both economically and as an element in the flora of the earth, all other living plants. The spermatophytes are the dominant plants of our time and exceed in number of species all the Thallophyta, Bryophyta, and Pteridophyta taken together.

The reason for the dominance of the Spermatophyta is clearly the fact that they are more effectively adapted to the land habitat than any other plants. Although the types of the three lower divisions which we have discussed in the preceding chapter, or the groups to which they belong, certainly do not represent an actual evolutionary series which has culminated in the production of the seed-bearing plants, they do probably correspond roughly to the principal steps in the evolution of the Spermatophyta.

It will be recalled that among the forms thus far studied the following progressive changes have taken place:

1. An increase in the size, complexity, differentiation, and independence of the sporophyte and in its adaptation to life on land.

2. A reduction in the quantity of the sporogenous tissue of the sporophyte relative to those tissues concerned with vegetative activity.

3. In plants above the bryophytes, a reduction in the size and an increase in the simplicity of the gametophyte generation. In *Selaginella* this has progressed so far that the gametophyte is dependent upon the sporophyte, much as the sporophyte was dependent upon the gametophyte in the liverworts and mosses.

4. In the pteridophytes, a lessening of the dependence of fertilization upon the presence of water, for in *Selaginella* the microspores with their contained male gametophytes are carried by gravity or air movements into very close proximity to the female gametophytes within the megaspores, and as a result the sperms need swim only a very short distance in order to enter the archegonia.

5. The retention of the megaspores within the megasporangium after their germination (in *Selaginella*), in contrast with the shedding of the spores before germination in most other pteridophytes. In

Selaginella the megaspores and contained female gametophytes remain within the sporangium until after fertilization has taken place, and in some species even until the embryo sporophyte is far advanced in its development.

6. Increasingly effective provision for spore dissemination.

The tendencies just enumerated reach their culmination in the seed plants, for:

1. The sporophyte of the seed plants may attain a length of hundreds of feet, it has the most highly complex differentiated tissues found among plants, and is dependent upon the gametophyte for a very short period only.

2. Although an immense number of spores may be produced, the tissue which is devoted to spore production is generally a very small fraction of the tissue of the sporophyte.

3. The male gametophyte is finally reduced in the seed plants to three cells, and the female gametophyte in the higher seed plants to eight cells, and both derive their food entirely from the sporophyte. Antheridia and archegonia, if represented at all, are very much reduced.

4. Fertilization is not conditioned by the presence of water, for the male gametophyte (shed microspore or pollen grain), carried by wind or insects to the vicinity of the megaspore, develops a tube (pollen tube) down which the male gametes pass to the female gametophyte. Except in a few very primitive seed plants, the male gametes have no cilia. With the loss of cilia by the male gametes there disappear the last structures which give direct evidence of the aquatic origin of the higher plants.

5. The megaspore (there is only one functional megaspore in each megasporangium) is never released from the megasporangium (ovule), but together with the female gametophyte, the embryo sporophyte, the megasporangium wall, and sometimes a mass of nutritive tissue (the endosperm), becomes the seed.

CHIEF DISTINGUISHING CHARACTERISTICS OF SPERMATOPHYTA

The two characteristics which most sharply differentiate the Spermatophyta from all other plants are (1) the formation of a pollen tube and (2) the production of seeds. These two characteristics are important factors making for the success of the seed plants, first, because the pollen tube has released them from dependence upon water for fertilization and, second, because the seed is a very efficient structure for reproduction and multiplication, being able to retain its vitality for many years (in some cases no doubt for as many as a hundred) and very

resistant to desiccation and to great extremes of temperature. Seeds are also well adapted for wide dissemination and, on account of the well-advanced state of development of the embryo sporophyte within the seed and the supply of stored food available to it, the new plant after germination is able to become well established before it must become self-supporting. These facts and the possession of very efficient organs and tissues for absorption, conduction, and conservation of water make it possible for seed plants to thrive in habitats which are much drier than those to which the Bryophyta and Pteridophyta are for the most part restricted.

FIG. 373.—Oak trees with mistletoe, a parasitic spermatophyte (*Phoradendron flavescens*), in dense clumps on the branches. (From Bureau of Plant Industry Bulletin.)

The seed-bearing plants include species which are adapted to a wide range of conditions. By far the majority are autophytic, but a few are heterophytic, as for example, such saprophytes as Indian pipe (*Monotropa*) and the Sierran snow plant (*Sarcodes*), and such parasitic forms as dodder (*Cuscuta*) and mistletoe (*Viscum* and *Phoradendron*). Autophytic seed-bearing plants are to be found in almost every location where organisms can exist at all. They are lacking in the following habitats:

1. The open sea, though many grow entirely or partially immersed in the shallow water along the seacoast.

2. The most precipitous of smooth, rocky cliffs, though some seem actually to prefer steep, rocky slopes.

3. The deeper parts of large bodies of fresh water, though they are found along the shores and extending to some distance into lakes, ponds, and slow flowing rivers.

4. The driest parts of certain deserts, where there is no rainfall.

5. Regions of perpetual snow, such as the summits of some peaks and the polar regions.

In addition to the typical terrestrial forms there are many aquatics, such as the water weed (*Elodea*) and marine eel-grass (*Zostera*), and a large number of epiphytes, mostly tropical or sub-tropical, such as the so-called Florida moss (*Tillandsia*) a member of the pine-apple family, and many orchids.

The seed plants have in all probability descended from pteridophyte ancestors, through forms long extinct which were intermediate between certain of the living ferns and the most primitive of the Spermatophyta. Inasmuch as the first part of this book was devoted very largely to an account of the morphology and the physiology of the sporophyte of the seed-bearing plants, we shall not discuss those subjects here. In this chapter we shall restrict ourselves for the most part to an account of the gametophyte generation of several types of the seed plants and to a statement of the homologies which exist between these plants and the Pteridophyta and Bryophyta.

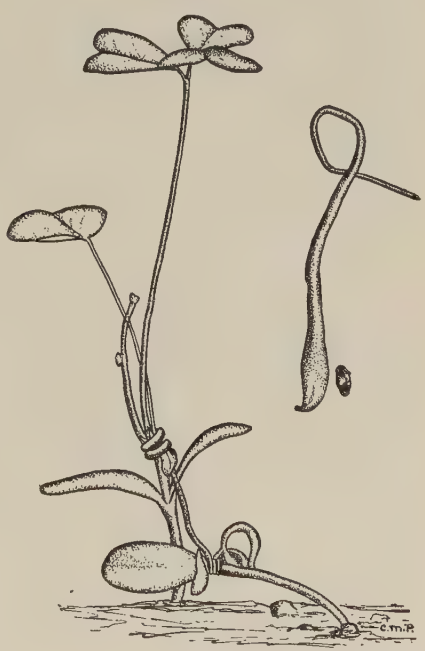


FIG. 374.—Dodder (*Cuscuta*), a parasitic angiosperm. To the right, a seed and a seedling of the parasite before its separation from the soil and its attachment to the host. To the left, two alfalfa seedlings already parasitized and the parasite no longer attached to the soil. (From Robbins and Eggington, Colorado Experiment Station Bulletin.)

The Spermatophyta consist of two well-marked classes, the Gymnospermae (gymnosperms) and the Angiospermae (angiosperms). These two class names are based upon one of the best-defined distinctions between the two groups. The seeds of the Gymnospermae (naked-seeded plants) are borne upon the surface of the megasporophyll (carpel or cone scale), while the seeds of the Angiospermae (covered-seeded

plants) are always formed within a closed structure (the ovary) formed by the union of the margins of one or more megasporophylls (carpels).

GYMNOSPERMAE

The gymnosperms are all woody, perennial forms and, with few exceptions, are evergreen plants. They are of great economic importance as sources of timber, rosin, and turpentine. The group is a relatively small one, including only about five hundred species, whereas there are more than 125,000 species of angiosperms. Among the best known gymnosperms are the pines (*Pinus*), spruces (*Picea*), firs (*Abies*), larches (*Larix*), junipers, frequently but incorrectly called cedars (*Juniperus*), the so-called Douglas fir (*Pseudotsuga*), and the redwood and big tree (*Sequoia*). We shall use the genus *Pinus* as a type of this group since its life history is better known than that of any other gymnosperm.

LIFE HISTORY OF PINUS (PINE)

The Sporophyte.—The familiar pine tree is the sporophyte plant and is homologous with the attached, dependent sporophyte (foot, seta, and capsule) of a moss and with the familiar fern plant (root, rhizome, and fronds). The most striking characteristics of the pine sporophyte are as follows: (1) excurrent branching; (2) retention of the leaves during the winter; and (3) the grouping of the long and slender needle-like foliage leaves in clusters or **fascicles** generally of two to five. Excurrent branching and the evergreen habit are characteristics of most gymnosperms, but the fascicles of leaves closely held together at the base by a circle of scales is peculiar to the pines. As in most of the common gymnosperms, the wood contains no tracheal tubes, but consists mostly of tracheids with many bordered pits. The linear form of the leaves, their very thick cuticle, and the depressed stomata show the pines to be xerophytic plants as are most of the gymnosperms.

The Strobili.—The sporophylls are borne in strobili or cones as in *Selaginella*, but megasporophylls and microsporophylls are not found in the same strobilus, as they are in *Selaginella*. Instead there are two kinds of strobili, megasporangiate and microsporangiate. (Fig. 375, 1, 2, 7, 8 and Figs. 376 and 379.) Because of the names commonly used for the megasporophylls (carpels) and for the microsporophylls (stamens) among the true flowering plants (angiosperms), the two kinds of strobili in the gymnosperms are often spoken of respectively as **carpellate** and **staminate** strobili or cones. They are borne upon the same individual plant.

FIG. 375.—Sugar pine (*Pinus lambertiana*). 1, twigs showing last year's foliage leaves, staminate (microsporangiate) strobili, and young leaves of this year's foliage; 2, a single staminate strobilus; 3 to 5, bracts and microsporophylls; 7 and 8, carpellate (megasporangiate) strobili; 9, megasporophyll as seen from below and showing the bract and the ovuliferous scale; 10, the same from above showing the megasporangia (ovules); 11 to 14, arrangement and structure of the needles (foliage leaves); 15, end of a twig showing one terminal and two lateral buds. (Copied by courtesy from Sargent in the *Silva of North America.*)

Megasporangiate Strobili and Megasporophylls.—The familiar pine cones are the carpellate or megasporangiate strobili. They remain on the tree for the greater part of two years in all pines, and in some for many years. These cones first make their appearance at the beginning of the growing season when the parts within the buds develop, and growth in length of the twigs begins. At the time there may be found near the tips of certain branches the newly formed miniature cones. They seldom exceed a centimeter in length and are generally deep red or flesh color. They consist of a central axis upon which the megasporophylls are spirally arranged. If one of the megasporophylls is removed from a strobilus and examined with a lens, it will be found to consist of a very short stalk and a scale to which a bract is attached on the lower side (Fig. 375, 9 and 10, and 378). On the upper side and near the base of the scale are two rounded or oval swellings. These are the megasporangia or ovules which eventually become the seeds. Sections cut lengthwise through an ovule show that it consists of an oval mass of tissue (the **nucellus**) surrounded by a single integument and with a micropyle which is directed toward the base of the scale (Fig. 378 *A*). At the opposite end from the micropyle, the tissue of the integument and nucellus is continuous with that of the scale.

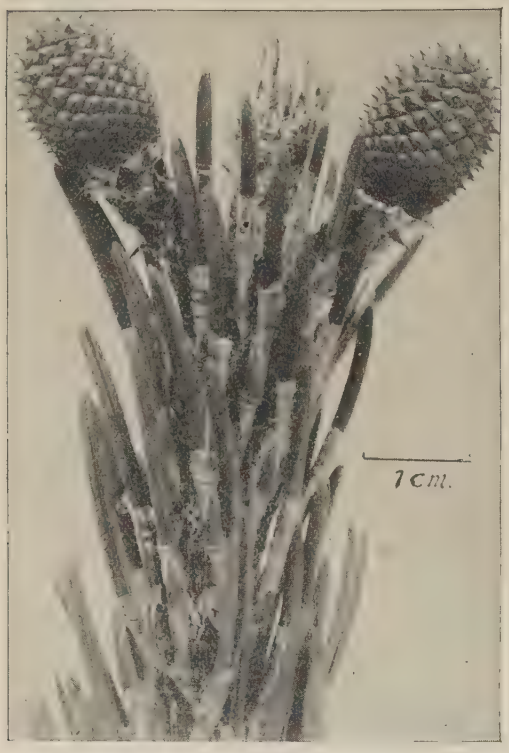


Fig. 376.—Tip of a branch of Monterey Pine (*Pinus radiata*), showing two megasporangiate strobili (carpellate cones) a short time after their appearance in the spring and about the time pollination takes place.

Microsporangiate Strobili and Microsporophylls.—The staminate or microsporangiate strobili are produced in much larger numbers than the carpellate cones and are smaller in size. They are found in

clusters near the ends of some of the branches. Like the megasporangiate strobilus, the microsporangiate strobilus consists of a short axis upon which are arranged the microsporophylls in a spiral fashion. They make their appearance at the beginning of the growing season.

FIG. 377.—Sugar pine (*Pinus lambertiana*). 1, mature cone; 2, single carpellate scale with two seeds attached; 3, single mature seed; 4, longitudinal section of seed, showing embryo embedded in endosperm; 5, embryo separated from seed, showing many cotyledons. (After Sargent from *Silva of North America.*)

The microsporophyll consists of a stalk, bearing at the end an expanded scale-like portion. To the under side of this scale and to the side of the stalk the two microsporangia (pollen sacs) are attached. Generally the microspores (pollen) are shed within a few weeks after the strobili have made their appearance whereupon the strobili, having performed their function, wither and soon fall from the tree.

Megasporangium and Megaspores.—Quite early in the development of the cone, sections of the nucellus (megasporangium) show near its center a single cell which is considerably larger than the surrounding cells

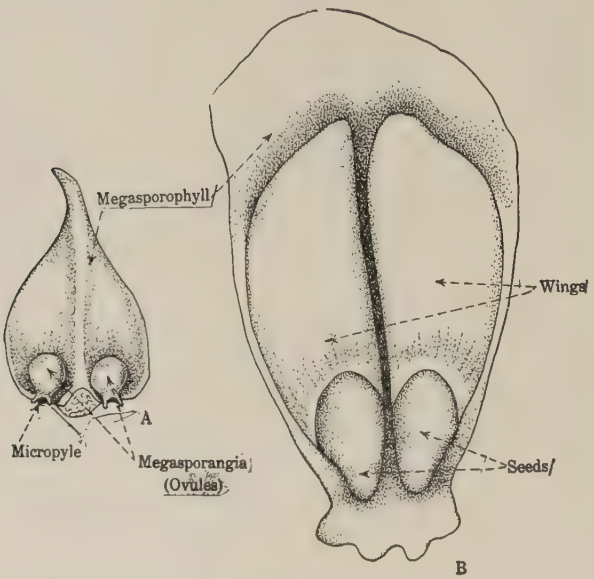


FIG. 378.—Megasporophylls of *Pinus*. *A*, about the time of pollination. *B*, after the seeds have matured. Note that the two drawings are made from different species.

and which has dense cytoplasm and a large nucleus. (See Figs. 381 *A* and *B*.) This is the megaspore mother cell. It will be recalled that in the megasporangium of *Selaginella* a number of megaspore mother cells are formed but only one formed megaspores. In *Pinus*, on the other hand, only one megaspore mother cell is formed and only one of the megaspores produced from it functions. The conspicuous spore mother cell within the nucellus of *Pinus* soon undergoes two successive divisions and thus four megaspores are formed. Instead of being arranged in a tetrahedral group as are the spores of all the Bryophyta and Pteridophyta and the microspore of the seed plants, these four

spores lie in a row as shown in Figs. 381 *D* and 382. All vegetative cells of the pine, including the spore mother, belong to the sporophyte generation and their nuclei have the diploid chromosome number. The first of the two nuclear divisions by which the megaspore mother cell gives rise to four megaspores is a reduction division such as we have already

FIG. 379.—Tip of a branch of *Pinus* bearing microsporangiate strobili (staminate cones). The strobili near the base of the cluster have already shed part of their pollen while in those in the upper part of the cluster the microsporophylls have not separated and no pollen has been liberated.

described in our account of the life history of a true fern. Accordingly, the megaspores have haploid nuclei. One of the four megaspores, the one farthest from the micropyle, now enlarges at the expense of the other three, which are finally completely absorbed. Although most

species of *Selaginella* which have been studied produce four megaspores in each sporangium there are species in which, as in *Pinus*, only one functional spore is formed. Thus, as in certain *Selaginella* species, only one functional megaspore is produced in each megasporangium.

Microsporangium and Microspores.—The development of the microspores within the microsporangia in *Pinus* is not essentially dif-

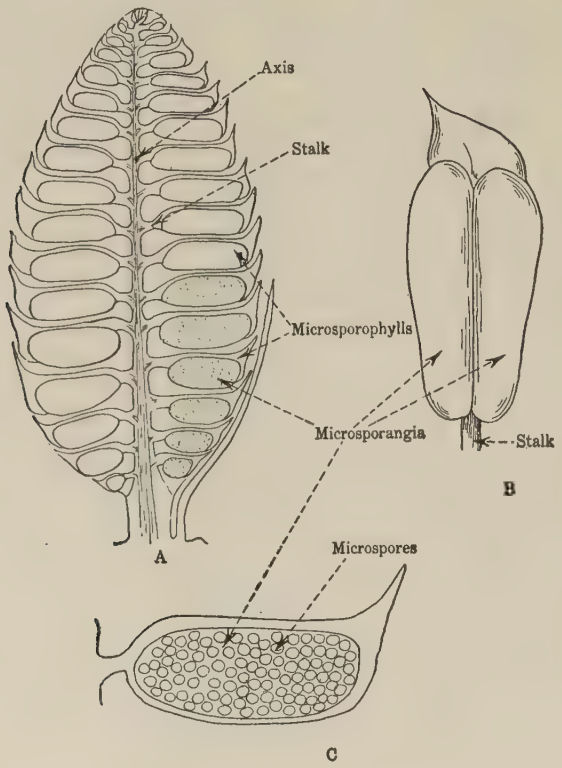


FIG. 380.—Microsporangiate strobilus and microsporophylls of *Pinus*. *A*, strobilus in longitudinal section. *B* and *C* two views of a microsporophyll, the latter in longitudinal section.

ferent from the corresponding process in *Selaginella* or from spore production in the true ferns. In order to study the early stages in the development of the sporangia and the spores, the rudimentary strobili must be dissected out of the terminal buds before the beginning of the season of active growth. In *Pinus Laricio*, at Chicago, Chamberlain found microspore mother cells as early as October of the year preceding the appearance of the strobili. The sporangium wall consists of several

layers of cells, of which the innermost at least is a tapetal layer such as is found surrounding the spore mother cells in the mosses and pteridophytes. The reduction division and the second division by which the tetrads of spores are produced take place early in the spring.

Germination of Microspores and Development of Male Gametophyte.—The pollen grains or microspores of *Pinus* germinate (that is, undergo nuclear divisions and thus begin the formation of the male gametophyte) as much as a month before they are shed from the micro-

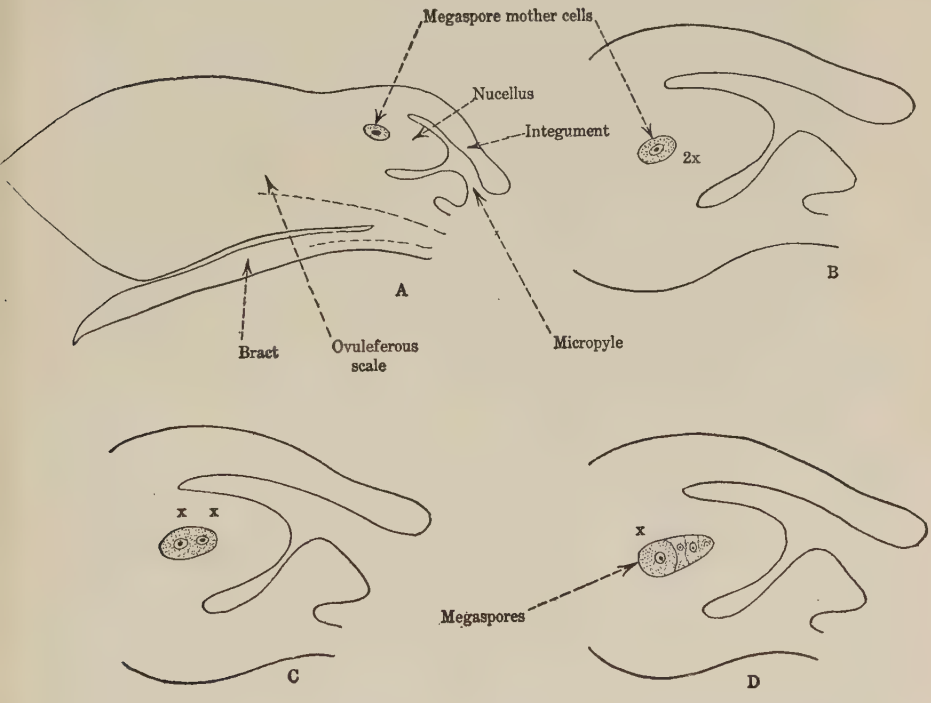


FIG. 381.—Diagrams showing the megasporophyll of pine in longitudinal section and the production of megaspores from the spore mother cell. (*A*, redrawn after Coulter and Chamberlain.)

sporangia. We shall describe the germination of the microspore before taking up the development of the female gametophytes, since it takes place months before the germination of the megaspore.

The microspore just before its germination consists of an oval cell with a single large nucleus. Each microspore has two balloon-like wings which are formed by the separation of the exine layer of the wall from the intine at two places and an inflation of the spaces thus formed between the two layers. The wings are air-filled and each may

at this stage be almost as large as the spore proper. Of the two nuclei formed by the first division of the single nucleus of the spore, one becomes flattened out against the spore wall and is soon cut off from the other daughter nucleus and from most of the cytoplasm of the spore by a thin cell wall. This nucleus, which we shall call the **first vegetative nucleus,** rapidly degenerates. Its sister nucleus has meanwhile undergone a second mitosis. Of the two resulting nuclei, one is the **second vegetative nucleus,** which behaves like the first vegetative nucleus and the other, together with the cytoplasm surrounding it, is called the **antheridial cell.** The two vegetative cells apparently perform no function but are merely vestigial cells corresponding to the vegetative cells which make up the greater part of the gametophyte of the ferns and to the single vegetative cell of the male gametophyte which develops within the microspore of *Selaginella.* A little before the microspores are shed the antheridial cell undergoes division into a smaller cell (the **generative cell**), cut off against the second vegetative cell, and a larger cell (the **tube cell**).

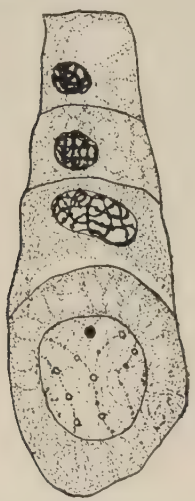


FIG. 382.—*Pinus austriaca.* Four megaspores which have arisen by the divisions of the megaspore mother cell within the nucellus. The large basal cell is farthest from the micropyle and is the one which gives rise to the female gametophyte. Redrawn after Ferguson.

Pollination.—About this time the microsporangia dehisce longitudinally and the pollen grains (microspores) are liberated. The quantity of pollen produced is astonishingly large. That shed by a single Scotch pine may be as much as a liter. It is yellow in color and resembles the finely powdered form of sulphur called "flowers of sulphur." There are records of pine pollen having been borne for hundreds of miles by the wind. Microscopic examination, at the time of pollen-shedding and for weeks after, of water, soil or the surface of plants anywhere in the vicinity of pines, will almost unfailingly reveal the characteristic pine microspores.

As in all wind-pollinated plants, by far the greater part of the pollen is wasted. Some does, however, reach the carpellate cones, the megasporophylls of which at this time are slightly separated, so that some of the microspores sift down between them and come to lie in close proximity to the micropyles of the ovules. Just at this time the nucellus in each ovule exudes a quantity of a sticky fluid, which protrudes

through the micropyle so that it comes in contact with some of the microspores. As the drop dries up, the pollen grain or grains are drawn down through the micropyle and come in contact with the nucellus itself. Pollination is accordingly different from that of the angiosperms in that the pollen grain, instead of being brought into contact merely with the stigma (tip of the carpel or carpels), is, in *Pinus* and many related gymnosperms, brought into direct contact with the megasporangium (nucellus of the ovule).

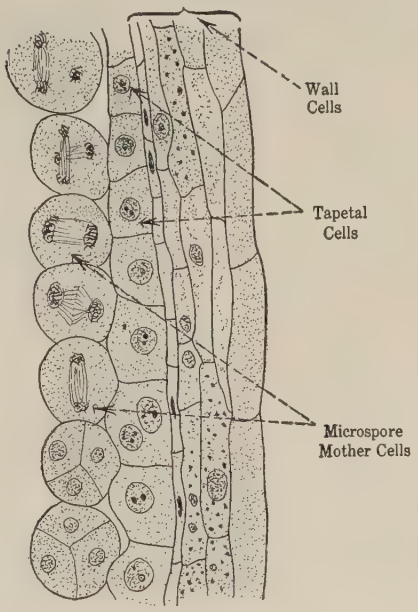


FIG. 383.—Part of a young microsporangium of *Pinus* showing divisions of the pollen mother cells. (Redrawn in part from Coulter and Chamberlain.)

Subsequent Changes up to Fertilization.—It will be recalled that at the time of pollination the pollen grain contains a male gametophyte consisting of two flattened and much disorganized vegetative cells, the generative cell and the tube cell (Fig. 384, *F*). The ovule is at this time in the condition already described, the nucellus of megasporangium proper being surrounded by a single integument and enclosing a single functional megaspore which is larger than the surrounding cells but lacks any thick spore wall such as is found in *Selaginella*. In *Pinus Laricio*, at Chicago, pollination was found to take place about the middle of June.

Very soon after pollination, the scales of the carpellate cone are pressed together as the result of their growth, the scales are sealed together by an exudation of pitch, and the whole cone is inverted by the curvature of its stalk. During the subsequent eleven months the male gametophyte does not develop to any considerable extent. A short pollen tube is formed by each pollen grain. This tube, which may branch somewhat, penetrates the tissue of the nucellus and grows downward very slowly until cold weather comes on.

Development of Female and Male Gametophytes.—During the year following pollination there is developed from the megaspore a considerable mass of tissue which is the female gametophyte, and is often spoken of as the endosperm. Its cells differ from those of the sur-

rounding nucellar tissue in that their nuclei have but half the chromosome number of the cells of the nucellus, since the latter belong to the sporophyte tissue.

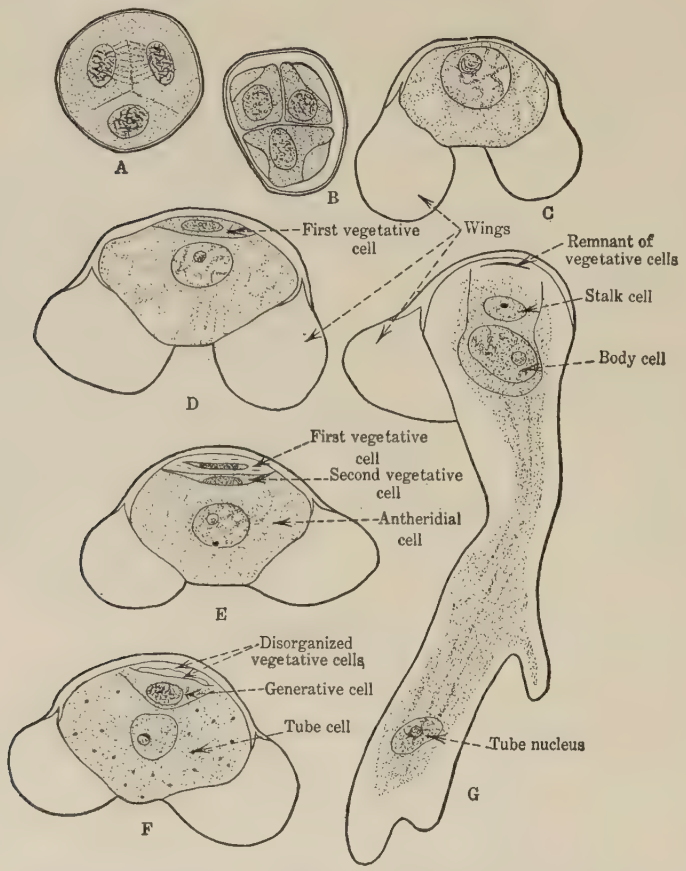


FIG. 384.—Successive stages in the development of the microspore and male gametophyte of *Pinus laricio*. *A*, showing the telophase of the second division of the spore mother cell. *B*, showing three of the four spores of a tetrad some time before maturity. *C*, a mature microspore. *D* to *F*, successive stages in the development of the male gametophyte up to the time the spores are shed. *G*, about a year after pollination and some time before fertilization. Figure 397 shows diagrammatically the nuclear divisions and other nuclear changes which accompany the development of the male gametophyte of *Pinus* and should be compared with Fig. 384. (Redrawn from Coulter and Chamberlain.)

In the development of this female gametophyte, or endosperm, the megaspore first enlarges considerably at the expense of the nucellar tissue which surrounds it. It then germinates, i.e., undergoes division of its nuc-

leus into two nuclei. These two nuclei are not separated by a wall, however, and they undergo repeated division without wall formation. After this (**free nuclear**) division has continued for some time, walls are formed between the nuclei and there results a solid mass of gametophyte tissue which has displaced a considerable amount of the tissue of the nucellus.

Late in the spring of the following year (nearly a year after pollination), there are formed at the end of the female gametophyte nearest the micropyle a number of archegonia, generally two or three, which are quite different in appearance from those of the Pteridophyta. The number of archegonia is much greater in certain gymnosperms, sixty for example in *Sequoia sempervirens*. Each archegonium has its origin in a single superficial cell of the gametophyte, and no part of it projects above the surface of the gametophyte. When fully developed, each archegonium consists of eight small neck cells in two tiers of four, and a very large cavity containing the egg cell, which almost fills it, and the ventral-canal cell. The ventral-canal cell disorganizes before fertilization. Neck-canal cells are entirely lacking. The cavity in which the egg lies is surrounded by a layer of cells, the **jacket cells,** which have dense cytoplasm and large nuclei and suggest the tapetal cells in sporangia. Although the function of the jacket cells seem to be similar to that of tapetum, it must be borne in mind that the tapetum is made up of sporophyte cells and nourishes the spore mother cells and spores, while the jacket cells belong to the gametophyte and supply food to the egg cell and later to the embryo.

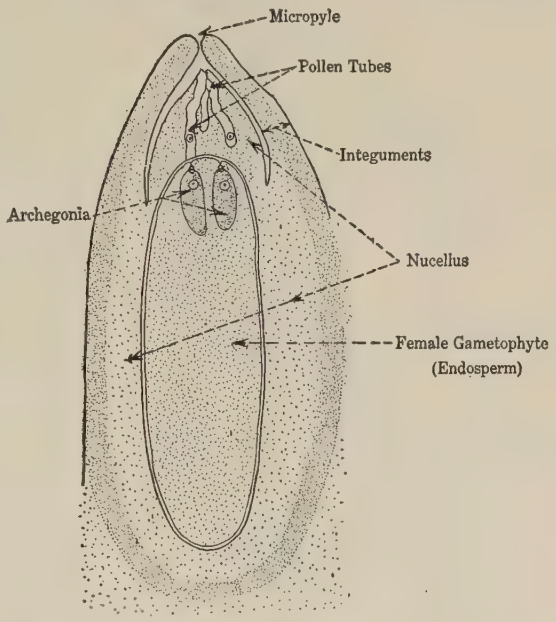


FIG. 385.—Ovule of pine at about the time of fertilization. (Redrawn after Coulter and Chamberlain.)

The archegonium is not fully developed and ready for fertilization until about a year after pollination. During the second spring the pollen

tube, which has ceased development during the cold winter months, has been growing slowly downward and penetrating the nucellar tissue which caps the apical portion of the female gametophyte. The tube nucleus has by this time passed from the body of the spore into the tube. Meanwhile, the generative cell has divided into a **stalk cell** and a **body cell** (Fig. 384 *G*), which also soon pass into the tube. In the tube the nucleus of the body cell divides into two nuclei which are the **sperm nuclei** and correspond to the sperms of *Selaginella* and other Pteridophyta and of the Bryophyta. Thus, the fully developed male gametophyte consists of two disorganized vegetative cells in the body of the spore and four cells which lie in the tube and are not separated from each other by cell walls. The cells in the tube are (1) the tube cell, (2) the stalk cell, and (3) two male or sperm cells. The nuclei of the gametes (sperm cells) are large and stain more densely than do the other nuclei in the tube, and their cytoplasm is quite clearly differentiated.

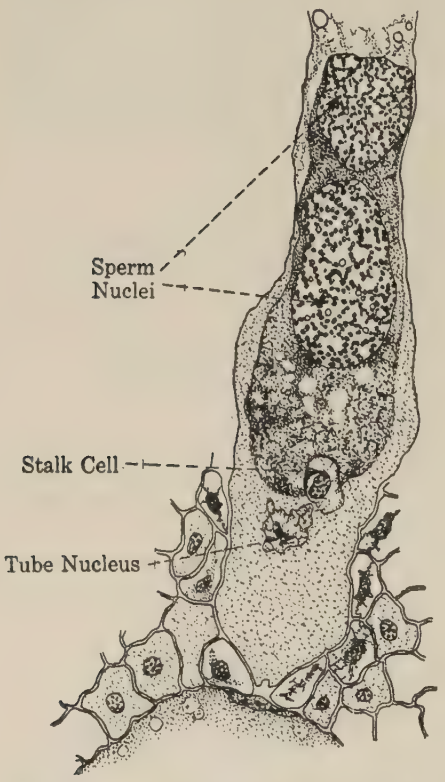


Fig. 386.—Tip of pollen tube of pine, just before it enters the archegonium. (After Ferguson.)

Fertilization.—When the tip of the pollen tube reaches the surface of the female gametophyte, it destroys the neck cells and discharges the four cells which it contains into the cytoplasm of the egg.

The nucleus of one (the functioning) male cell now moves toward the large egg nucleus which lies deep in the cytoplasm of the egg cell, and fusion of the two gamete nuclei takes place. The non-functioning male nucleus and the tube and stalk nuclei soon undergo dis-

organization, their material becoming part of the food store of the zygote.

Formation of the Embryo.—Immediately upon the fusion of the functioning male nucleus and the egg nucleus, the first division of the zygote nucleus begins. In this division twenty-four chromosomes (the sporophyte number) of which twelve (the gametophyte number) were contributed by the nucleus of the male cell and twelve by the egg nucleus,

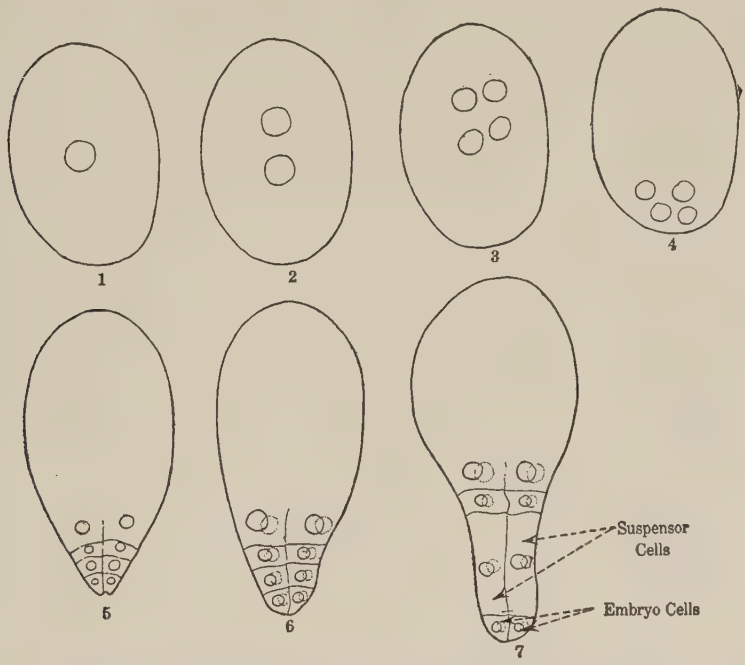


FIG. 387.—Diagrams showing stages in the development of the proembryo of *Pinus* from the zygote; 1, shows the zygote before the first division of the fusion nucleus; 2 to 7, see explanation in the text.

are involved. These split so that each daughter nucleus of the zygote receives twenty-four chromosomes. A second mitosis then takes place and thus four free nuclei are formed. These pass to the base of the egg cell where each nucleus divides again. During this division, walls are formed between the resulting eight nuclei which lie in two tiers of four. By later divisions sixteen cells (four tiers of four) are produced, of which the uppermost four are not cut off from the cytoplasm of the egg (Fig. 387, 4, 5, 6). This group of sixteen cells is called the **pro-embryo.** Of the four tiers of cells of the pro-embryo, those in the next to the lowest tier elongate to ten or twelve times their original length (Fig. 387, 7 and

388, *A*). They are called **suspensor cells** and their elongation causes the four cells of the lowermost tier to be pushed deep down into the endosperm (female gametophyte tissue) below the archegonium. The eight cells of the two upper tiers remain within the cavity of the original egg cell and serve to absorb food for the nourishment of the four embryo cells, each of which develops into an embryo. Since there may be three archegonia within a single pine ovule, as many as twelve young embryos may thus be formed. Before their development has progressed far, one generally surpasses the others and finally develops at their expense into the one functioning embryo of the seed.

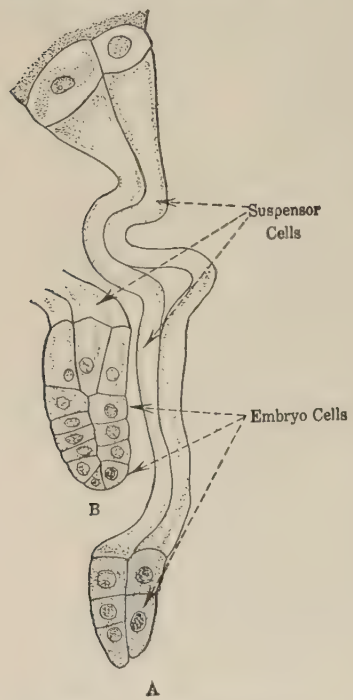


FIG. 388.—Further development of the proembryo of pine, showing early stages (*A* and *B*) in the development of the embryos. (Redrawn after Coulter and Chamberlain.)

The Seed.—Even after fertilization the endosperm continues to grow, encroaching upon the tissue of the nucellus and absorbing it. Accordingly, in the ripe seed nothing remains of the nucellus but a brown, papery layer capping the endosperm at the micropylar end of the seed. Buried in the endosperm of the mature seed is the embryo, which consists of the **radicle,** the **hypocotyl,** three to many **cotyledons,** and the **plumule.** The shell, or seed coat, of the pine seed is formed by changes in the tissue of the integuments. In many pines a layer of tissue from the upper surface of the cone scale splits off to form a wing, which remains attached to the base of the seed when it is shed. This imparts a spinning motion to the seed as it falls, and slows up its rate of descent so that in a moderate breeze the seeds may be carried some distance from the tree on which they are produced. The germination of pine seeds does not differ in any very significant particular from that of the angiosperm seeds discussed in an earlier chapter. After fertilization and while the ovule is developing into a seed, the whole carpellate cone grows to many times its previous size and the tissues of the cone scales become woody and hard and lose most of their water. In most species the scales separate after the seeds have have become mature, and allow the seeds to escape.

SUMMARY OF THE PRINCIPAL FEATURES OF THE LIFE HISTORY OF PINE

(1) **Formation of microspore mother cells within the microsporangia,** two of which are borne upon each microsporophyll of the staminate strobilus.

(2) **Formation of a tetrad of microspores from each microspore mother cell** by two divisions, of which the first is a reduction division and marks the beginning of the male gametophyte generation.

(3) **Germination of the microspores within the microsporangium.** At the time these spores are shed the male gametophyte consists of two disorganized vegetative cells, a tube cell and a generative cell.

(4) **Appearance within the ovule** (which consists of megasporangium or nucellus and an integument) **of a single conspicuous megaspore mother cell.**

(5) **Division of this cell to form a row of four megaspores,** the first division being a reduction division and marking the beginning of the female gametophyte generation, and the development of one of these megaspores at the expense of the other three until it becomes the sole functioning megaspore.

(6) **Escape of microspores, and pollination by wind.** The microspores sift down between the megasporophylls and come to lie near the megasporangia. They are drawn in through the micropyle to the surface of the nucellus by the retraction of a mucilaginous drop protruding from the micropyle at the time of pollination.

(7) **Formation of a pollen tube, which grows slowly downward through the tissue of the nucellus.** It develops short, irregular branches which appear to act as haustoria and absorb food from the nucellus tissue. The growth of the pollen tube ceases during the winter but is resumed the following spring.

(8) **Germination of the megaspore and growth of the female gametophyte** at the expense of the tissue of the nucellus. **Formation** at the apical end of the **female gametophyte** (endosperm) **of several archegonia** of much simpler form than those of the Pteridophyta.

(9) **Entrance of the pollen tube and discharge of its contents into the egg cell of the archegonium.** This takes place about a year after pollination. The cells from the pollen tube are the tube cell, the stalk cell and two male cells, the latter three derived from the generative cell mentioned (in 3) above. One male nucleus fertilizes the egg nucleus (this initiates the sporophyte generation), and the other nuclei undergo disorganization.

(10) **Immediate development of the zygote into a pro-embryo of sixteen cells,** four of which are embryo cells and four suspensors which

elongate and thrust the embryo cells deep into the tissue of the endosperm (female gametophyte). Each embryo cell begins to develop into an embryo, but one of the many embryos gains the upper hand and becomes the single functioning embryo of the seed.

(11) **Development of the ovule into a seed,** involving growth of the embryo, further growth of endosperm with almost complete disappearance of the nucellus, and formation of the hard outer layer or shell of the seed.

(12) **Germination of the seed.**

(13) **Growth into a mature sporophyte plant** producing each season microsporangiate strobili and megasporangiate strobili.

Other Gymnosperms.—What has been said of the structure and life history of *Pinus* applies in its principal features to most of the common gymnosperms which belong to the Order Coniferales. To point out the principal variations from the *Pinus* type within this order would be beyond the scope of this book. The other three orders of the living Gymnosperms (Cycadales, Ginkgoales and Gnetales) differ in a number of interesting and important particulars from *Pinus*, and nearly related genera. We shall give special attention to the Cycadales because they are probably the most primitive of living Gymnosperms. In this order the plant body (sporophyte) consists of a stout stem which branches sparingly or not at all and bears a rosette of leaves at the ends of the stems. The plants have the appearance of tree ferns or palms.

The cycads are dioecious in the sense in which that term is used among the seed-bearing plants; that is to say, the microsporophylls and megasporophylls are borne upon different individual plants. The microsporophylls bear numerous microsporangia (as many as 750 in the genus *Dioon*) and thus are in striking contrast with those of *Pinus* which bear only two microsporangia. In some the megasporophylls show a distinct resemblance to vegetative leaves. In most of the genera only two megasporangia are borne on each megasporophyll. In *Cycas*, *Zamia*, and other genera of the Cycadales as well as in *Ginkgo biloba*, the only living species of the Ginkgoales, the male gametes have cilia and are able to swim like the sperms of the Pteridophyta and Bryophyta. These gymnosperms with motile sperms partly bridge the gap between the heterosporous Pteridophyta and the seed-bearing plants.

We shall discuss briefly the life history of *Zamia*, a typical Cycad.

The megasporangium consists of a nucellus enclosed by a relatively thick integument. Formation of the megaspore mother cell and of four megaspores, of which only one functions, is essentially the same as in *Pinus*. The megaspore on germination gives rise to a mass of tissue, the female gametophyte, consisting, as in *Selaginella*, of small cells at the

micropylar end, and of larger cells, nutritive in function, at the opposite end. Usually four archegonia, similar in most respects to those of *Pinus*, are found in each gametophyte.

The microsporangia and the development of the microspore tetrads are not essentially different from that in *Pinus*. The principal differences in the male gametophyte are that in *Zamia* (1) only one vegetative cell is produced, (2) this vegetative cell does not degenerate at once but remains alive until the time of fertilization, and (3) the sperms or male gametes are provided with a large number of cilia and swim around in the pollen chamber for a time before fertilization takes place.

Following fertilization there is rapid free nuclear division resulting in many nuclei, which move towards the lower end of the egg. Walls are formed about the nuclei in this region, giving rise to a tissue known as the **pro-embryo.** In the upper part of the egg, numerous nuclei remain free for a period. Certain cells in the pro-embryo now begin to elongate, forming a **suspensor** which pushes the tip cells of the pro-embryo out of the archegonium, bringing them in contact with the nutritive tissue of the female gametophyte (endosperm). The cells at the end of the long suspensor develop into the embryo which has two cotyledons, a stem growing point between them, a short hypocotyl and a radicle.

In the mature seed, the embryo sporophyte lies embedded in the endosperm (remnant of the female gametophyte) which is surrounded by the remains of the nucellus, which in turn is enclosed by the seed coats, consisting of an inner stony layer and a soft outer one.

In certain particulars *Zamia* is a plant with characters intermediate between those of the Pteridophyta and those of the higher Gymnosperms, of which *Pinus* is a type. Cycad features, reminiscent of Pteridophyta are as follows:

1. Pinnate foliage leaves, which exhibit a spiral inrolling.
2. Concentric vascular bundles in leaf veins and axes of strobili.
3. Leaf-like megasporophylls in certain groups.
4. Motile sperms.

Cycad characters similar to those of the higher gymnosperms are as follows:

1. Vascular bundles in stems of a gymnosperm type.
2. Reduced gametophytes.
3. Woody sporophylls in certain groups.
4. Pollen tube.
5. Pro-embryo.
6. Seeds.
7. Complete elimination of neck-canal cells in archegonia.

Ginkgo biloba (order Ginkgoales) is the so-called "maidenhair tree," long cultivated in China and Japan and now to a considerable extent in this country. It is different from the Cycadales in being freely branched and bearing simple leaves which are fan-shaped and strongly suggest the leaflets of the maidenhair fern. Ginkgo is dioecious, and the microsporophylls and megasporophylls are much reduced and not leaf-like.

The Gnetales in several respects are more like the angisoperms than are any of the other gymnosperms. Thus they have true vessels in the secondary wood; the groups of microsporophylls and megasporophylls

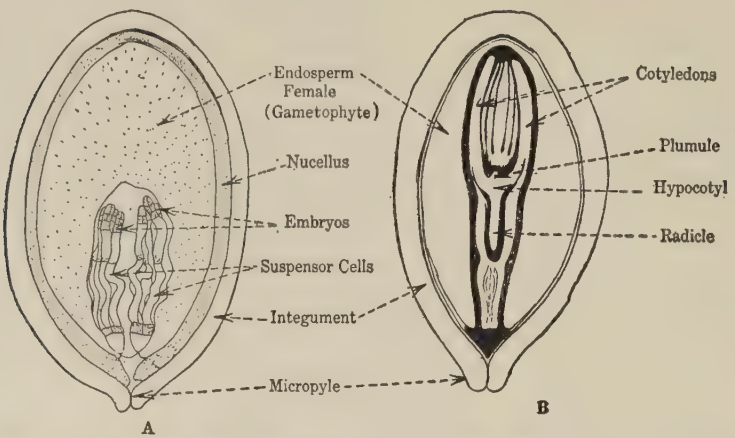


FIG. 389.—Two stages in the development of the pine seed shown in longitudinal section. *A* is much more highly magnified than *B* and shows a much earlier stage of development. Note the numerous embryos in *A* and the single surviving embryo in *B*, also the great relative reduction of the nucellus in the older seed. (Redrawn from Curtis.)

are borne on the same plant; and in two of the three genera (*Tumboa* and *Gnetum*) there are no archegonia formed and the female gametophyte shows striking resemblances to the embryo sac (female gametophyte) of the angiosperms.

Comparison of Selaginella, Zamia and Pinus.—

1. The sporophyte of *Zamia* and *Pinus* is very much larger, longer lived, more complex, and better adapted to terrestrial life than that of *Selaginella*.

2. Megasporangia and microsporangia are produced on different strobili in *Zamia* and *Pinus* and on the same strobilus in *Selaginella*.

3. The male gametophyte of *Pinus*, though it has two vegetative

cells as compared with one in *Selaginella* and *Zamia*, is simpler than that of *Selaginella* and *Zamia*, for it lacks any definitely organized antheridium.

4. In *Selaginella* the male gametes are ciliated and swim in water to the archegonia; in *Zamia* they are ciliated but pass down a pollen tube to the pollen chamber where they swim around for a time before fertilization, while in *Pinus* they are not ciliated and pass down a pollen tube to the archegonia.

5. There is but a single functioning megaspore in each megasporangium of *Pinus* and *Zamia*, while in most species of *Selaginella* there are four.

6. The megaspores of *Selaginella* finally leave the megasporangium, even though this may not take place until after germination, fertilization, and embryo formation have taken place. In *Pinus* and *Zamia* the megaspore never leaves the megasporangium.

7. The archegonia of *Pinus* and *Zamia* are even simpler and more reduced than are those of *Selaginella*.

8. In *Selaginella* and *Zamia* only a short period intervenes between liberation of the microspores and fertilization, while in *Pinus* almost a year passes between pollination and fertilization.

9. In *Pinus* the zygote gives rise to four embryo sporophytes; in *Zamia* and *Selaginella* to only one.

10. *Selaginella* gives rise to no such structure as the seed of *Pinus* and *Zamia* which consists of embryo sporophyte, female gametophyte (endosperm), and part of the tissue of the megasporangium.

ANGIOSPERMAE

The second class of the Spermatophyta, the Angiospermae, far exceed in number of species and in their importance to man any other class in the Plant Kingdom. In fact, in the number of described species the angiosperms exceed all the other plant groups taken together. The group includes, with the exception of certain gymnosperms which furnish timber, turpentine, and rosin, practically every plant that is utilized by man as a source of food, clothing or materials for use in industry and in the arts. Although they include some very simple forms, which have evolved by reduction from more highly differentiated forms, they represent without question the highest point in the evolution of plants.

The angiosperms as a class are better adapted to the land habitat than any other class of plants, and accordingly are not only the most important and conspicuous element in the flora of the earth but are rep-

resented in practically every part of the world where plants can live at all.

Distinction between Gymnosperms and Angiosperms.—Although angiosperms have much in common with the gymnosperms, the two classes are quite distinctly marked off from each other. The principal points of contrast are:

1. Whereas the gymnosperms are all woody, perennial plants, the angiosperms also include, in addition to such forms, many herbaceous annual and biennial plants.

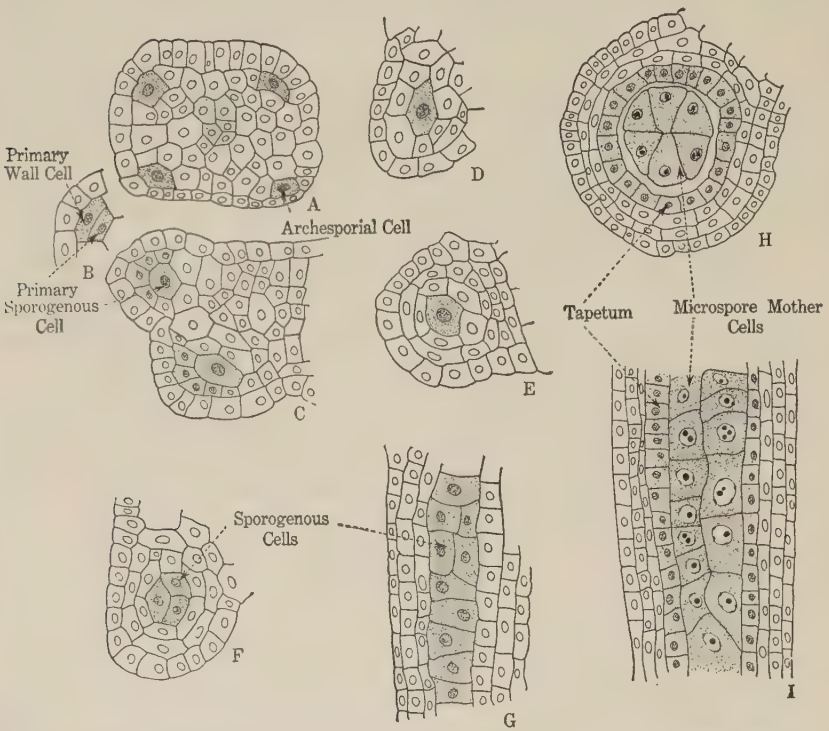


FIG. 390.—Stages in the development of the anther of wheat. *A*, cross section of young anther. *B*, first division of archesporial cell. *C*, *D*, *E* and *F*, cross sections of anthers showing subsequent division. *G*, longitudinal section of *F*. *H* and *I*, cross and longitudinal sections of a locule of a young anther, showing mature microspore mother cells. (Redrawn from Percival.)

2. In typical angiosperms, microsporophylls (stamens) and megasporophylls (carpels) are borne together in groups (flowers), while in the gymnosperms, as we have already learned, they are borne in different groups (staminate and carpellate strobili).

3. With very few exceptions, tracheal tubes occur in the xylem of all angiosperms, but they are lacking in the xylem of all living gymnosperms except the *Gnetales*.

4. Angiosperm seeds are borne within a closed structure (ovary) presumably resulting from the fusion of the edges of one or more megasporophylls, while the seeds of the gymnosperms are borne naked on the surface of megasporophylls, which do not form ovaries.

Life History of Wheat (*Triticum*).—In our discussion of the different major groups of plants, it has been the plan to trace in detail the life

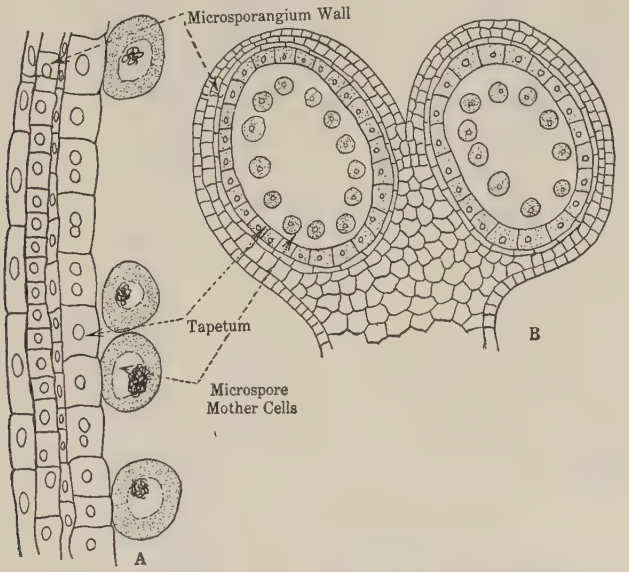


FIG. 391.—*A*, longitudinal section of a portion of the wall of the anther of wheat. *B*, transverse section of an anther lobe of wheat. (Redrawn from Percival.)

history of some one genus, which is fairly representative of the group under consideration. This has been supplemented by a statement of the principal departures, which occur within that group, from the type representative. Among the several thousand genera of angiosperms, there is for the most part marked uniformity in the essential stages of their life history. As the angiosperm representative, we have chosen *Triticum aestivum* (common wheat) not only because its life history has been rather completely worked out, but also because it is one of the most important and familiar plants in the world.

As in the Pteridophyta and in Gymnospermae, the sporophyte of wheat, and of other angiosperms, is the conspicuous generation in the life history; i.e., the sporophyte is " the wheat plant."

Inasmuch as the first half of this book was almost entirely devoted to an account of the structure and physiology of flowering plants, it will not be necessary for us to describe here the mature angiosperm sporophyte. It will be recalled that the plant body of an angiosperm consists of a root, and shoot, the latter made up of the stems and leaves, and that in addition to foliage leaves there are floral leaves.

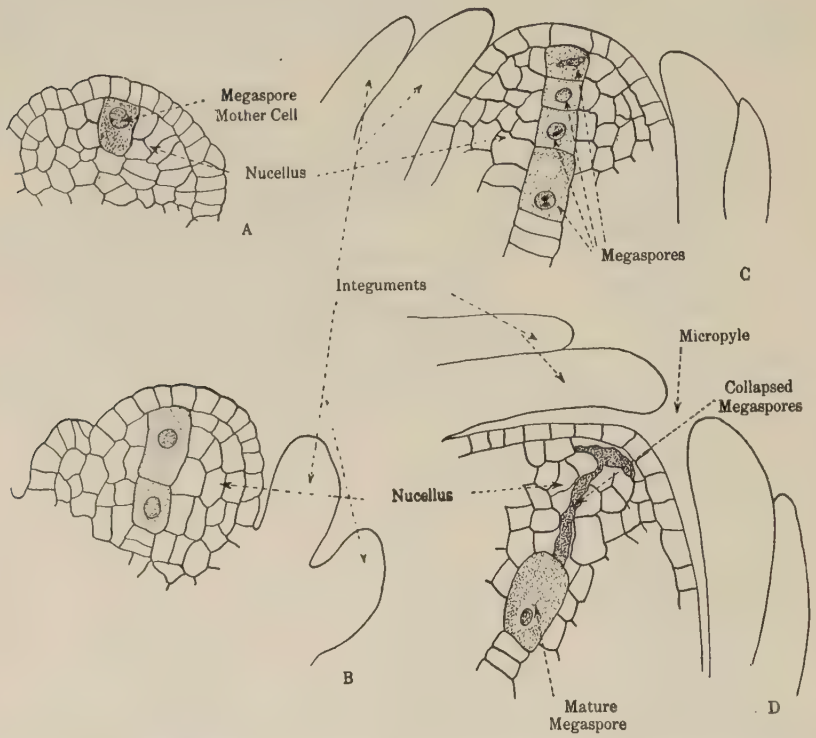


FIG. 392.—Median lengthwise section of young ovules of wheat, showing development of the megaspores and the degeneration of all but one of these. (Redrawn from Percival.)

The principal features of the grass flower were described on pages 255–257. The stamens and carpels are respectively homologous with the microsporophylls and megasporophylls of *Pinus* and *Selaginella*. In this chapter we shall use the terms microsporophylls and megasporophylls rather than the terms stamens and carpels which originated long before the homology of these structures with the spore-bearing leaves of the gymnosperms and pteridophytes was first suspected.

Microsporophylls and Microsporangia.—The anther consists at first of a small mass of meristematic cells (Fig. 391). There are early differentiated in this mass four separate groups of cells which by further

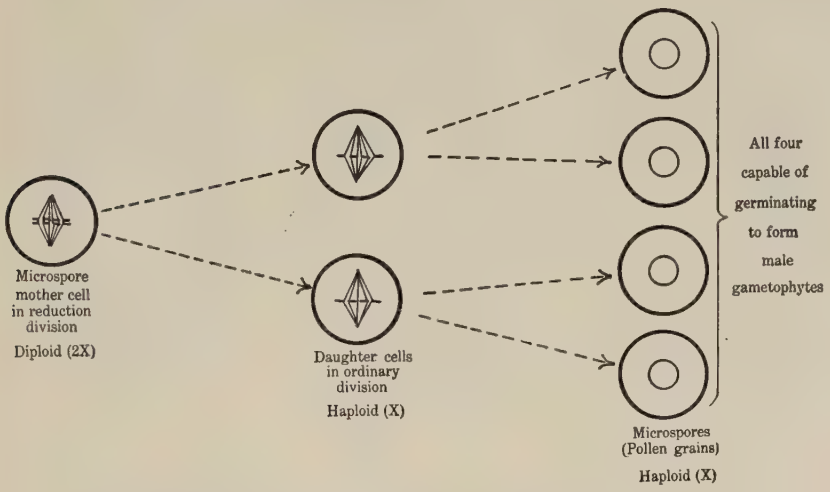


Fig. 393.—Diagram showing the development of microspores from a microspore mother cell. Compare with Fig. 396.

development will become the microsporangia. Each of these groups of cells has its origin in a longitudinal row of cells just beneath the epidermis. Each cell of this row divides, by a wall parallel to the surface of the anther, to form two rows of cells. By further division of the cells of the outer row, several layers of cells are formed, and these, together with the epidermis, make up the wall of the microsporangium. The innermost wall layer is the tapetum. The tapetum breaks down during the development of the microspores, its protoplasm furnishing food for the development of spores. By repeated division of the cells of the inner of the two longitudinal rows, microspore mother cells are formed. Each mother cell now undergoes two successive cell divisions, during the first of which there is a reduction in the number of chromosomes, in a manner similar to that described on page 502ff. Thus, each mother cell gives rise to four microspores (pollen grains).

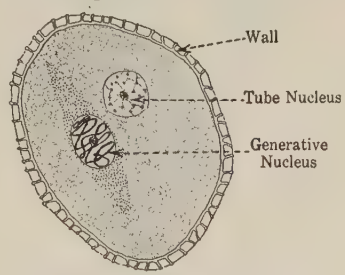


Fig. 394.—Pollen grain (microspore) of *Lilium* at the time of shedding.

Megasporophylls and Megasporangia.—The megasporangium (nucellus) has its origin in a small mass of undifferentiated cells which protrude from the placenta. From the base of this projection arise two rings of tissue which grow up about the developing megasporangium.

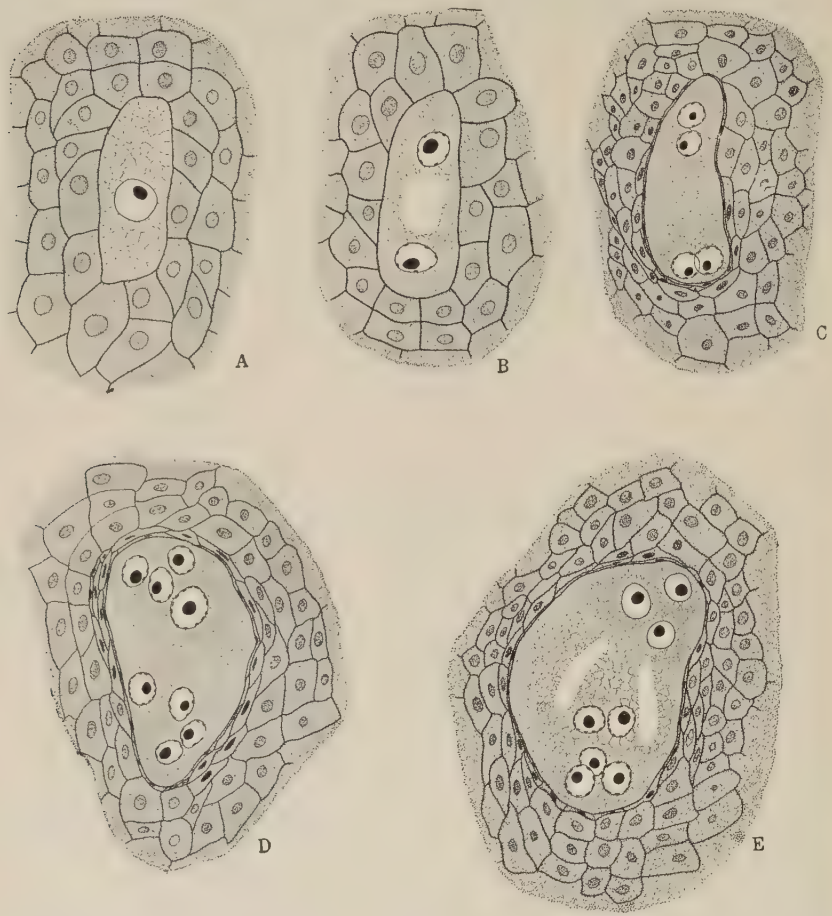


FIG. 395.—Stages in the development of the female gametophyte (embryo sac) of corn. Longitudinal sections. *A*, megaspore mother cell. *B*, 2-celled embryo sac. *C*, 4-celled embryo sac. *D*, 8-celled embryo sac at time the polar nuclei have started to migrate. *E*, 8-celled embryo sac after the polar nuclei have migrated. The megaspore mother cell and embryo sacs are embedded in nucellar tissue. (Redrawn from Miller, in *Journal of Agricultural Research*.)

These two layers of tissue (the integuments) finally entirely envelop the megasporangium proper, except for a small opening (micropyle) at the free end of the ovule (Fig. 392 *D*).

While the megasporangium is still very small, one of the cells just below the epidermis of the nucellus becomes differentiated from the surrounding cells in size, and in the appearance of its contents. This is the megaspore mother cell, and the nucellar tissue surrounding it constitutes the megasporangium wall. No tapetal layer is formed.

The nucleus of the megaspore mother cell now undergoes two successive divisions and thus four potential megaspores are produced. These spores are not arranged in the characteristic tetrahedral groups, as are the spores of all Bryophyta and Pteridophyta and the microspores of seed plants, but in a straight row. As the first of the divisions by which the four spores arise is a reduction division, the spore mother cell

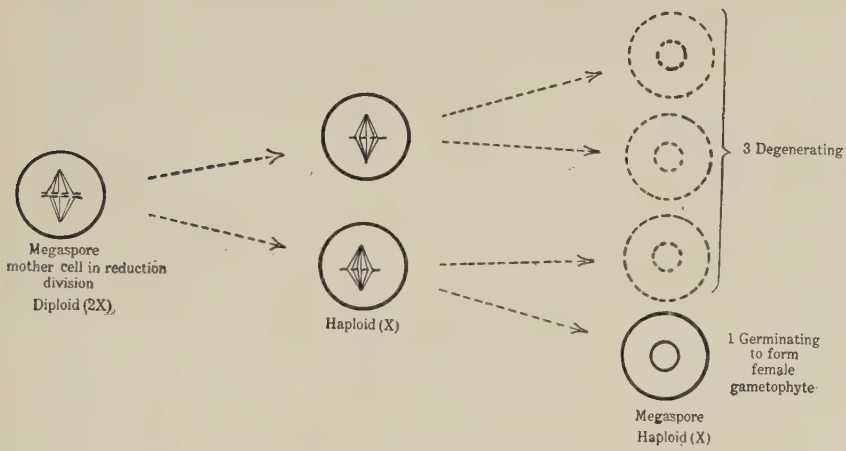


FIG. 396.—Diagram showing the development of megaspores from the megaspore mother cell. Compare with Fig. 393.

is the last cell in the life cycle having the diploid chromosome number, the spores having the haploid nuclei. Definite walls are formed around each megaspore. Soon the basal megaspore begins to enlarge at the expense of the other three, and finally these three are completely absorbed, leaving a single large functioning megaspore, as in *Pinus*.

The Male Gametophyte.—**Germination of the microspore** begins while it is still within the microsporangium. For convenience we shall consider the germination of the microspore and the development of male gametophyte as taking place in the following stages:

(1) **Division of the protoplast of the microspore into a tube cell and a generative cell.** The cytoplasm of these two cells is clearly differentiated, but they are not separated by a wall. (See Fig. 394.)

(2) A little later, and before the shedding of the microspores, the **generative cell divides to produce two male gametes.** (In many angiosperms the second division does not take place until after the pollen tube is formed.)

(3) **Following pollination, the formation of the pollen tube.**

(4) **Migration of the two male gametes into the pollen tube,** and sometimes the migration of the tube nucleus as well.

The mature male gametophyte, consisting of three nuclei and some associated cytoplasm, is even more reduced than that of *Pinus,* for in the latter case there are, in addition to the two sperm nuclei, two vegetative cells, a tube cell, and a stalk cell.

The Female Gametophyte (*Embryo Sac*).—The protoplast of the megaspore, as in *Pinus* and *Selaginella,* now undergoes free nuclear division. There results a female gametophyte consisting of eleven to fifteen nuclei lying free in a mass of vacuolate cytoplasm. In contrast with *Pinus* and *Selaginella,* in the angiosperms, cell walls are not subsequently formed between the nuclei of the female gametophyte.

This process of development of the female gametophyte may be conveniently divided into the following stages:

(1) The **first division of the megaspore nucleus results in two nuclei, which promptly separate,** and one of which moves to the micropylar end of the sac, and the other to the opposite (antipodal) end of the sac.

(2) **Each of these two nuclei divides,** so that there are **two nuclei at the micropylar end,** and **two at the antipodal end.**

(3) Following this second division, **each of the four nuclei divides,** resulting in eight nuclei, **four at the micropylar end** and **four at the antipodal end.**

(4) Now, **a single nucleus from each group** of four **moves toward the center of the embryo sac.** The two nuclei (polar nuclei) lie in contact with one another without fusing until the time of fertilization.

(5) **The three nuclei at the end opposite the micropyle divide, forming a group of six to eight antipodal nuclei.** Although not separated from one another by cell walls, each of these nuclei has about it a quantity of cytoplasm set off from that of neighboring nuclei, so that we may speak of them as cells (the antipodal cells). In most angiosperms there are only three antipodal cells.

(6) Of the **three nuclei remaining at the micropylar end,** one is the **egg nucleus,** and the other two are the **synergid nuclei.** Each of these nuclei has associated with it a quantity of cytoplasm, which is separated by a limiting membrane from the rest of the embryo sac. Thus at the time of fertilization the female gametophyte of wheat consists of:

(*a*) **Two synergids** or "helper cells" at the micropylar end of the embryo sac.
(*b*) **A single egg cell** near the synergids.
(*c*) **Two polar nuclei,** usually near the center of the embryo sac.
(*d*) **Six to ten antipodal cells,** at the end of the embryo sac opposite the synergids.

Pollination and Development of the Pollen Tube.—The pollen of wheat is carried to the plume-like stigma by the wind. Within one hour and a half to two hours after pollination, the pollen tube begins to develop.

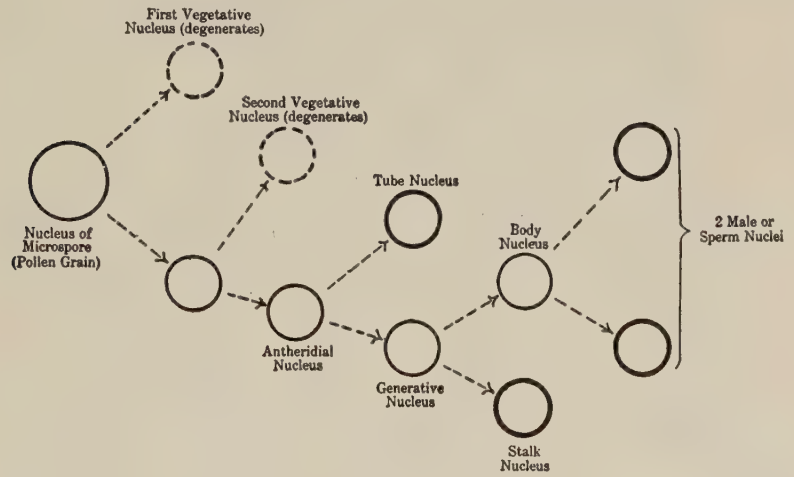


FIG. 397.—Diagram showing nuclei formed during development of the male gametophyte from a microspore of a pine. This figure properly belongs on page 530.

It penetrates the tissue of the stigma and, entering the hollow style, grows downward into the ovary, and finds its way to the micropyle. After passing through this opening, it penetrates the tissue of the nucellus and enters the embryo sac.

There is considerable variation in different angiospermous plants as to the length of the interval between pollination and fertilization. In wheat the union of the gamete with the egg nucleus has been observed between thirty and forty hours after pollination. In most herbaceous angiosperms, the interval is a few hours or days. In the elms, oaks, beeches, walnuts, orange and other species of *Citrus*, and many other woody plants, the interval may vary from one to eleven months.

Fertilization.—After entering the embryo sac, the pollen tube grows towards the egg nucleus. The tip of the tube is then ruptured and its

contents discharged. **One of the sperm nuclei fuses with the egg nucleus** and the **second sperm nucleus unites with the polar nuclei to form a primary endosperm nucleus.**

At the union of a sperm nucleus with the egg nucleus, there is a **doubling of the number of chromosomes,** and the **resulting zygote marks the beginning of the new sporophyte generation.** At the union of the second sperm nucleus with the two polar nuclei, there is a trebling of the number of chromosomes. The resulting "**triple fusion nucleus**" develops into endosperm ($3x$ tissue).

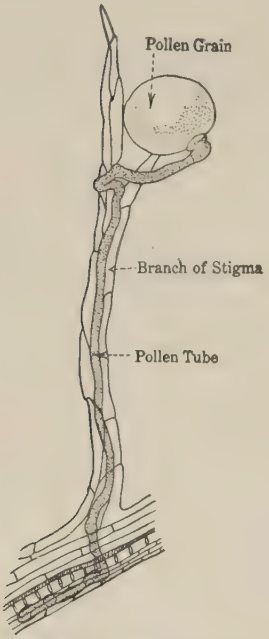


FIG. 398.—Single hair of the stigma of corn (*Zea mays*), showing path of the pollen tube. (Redrawn from Miller, in *Journal of Agricultural Research.*)

By the union of the sperm with the egg, the zygote is furnished with one set of chromosomes from the male parent and another set from the female parent. These two sets are associated in all the cells of the sporophyte. That is, in the first division of the zygote nucleus and in all subsequent divisions of sporophytic cells, chromosomes of paternal origin (contributed by the sperm nucleus) and those of maternal origin (contributed by the egg nucleus), split longitudinally and each daughter nucleus receives an equal amount of both maternal chromatin and paternal chromatin. There is reason to believe that the chromatin contributed by the male and female gametes respectively maintains its individuality in the nuclei of all sporophyte cells.

The synergids degenerate at about the time of fertilization. During the growth of the embryo and endosperm, the antipodal cells also slowly degenerate.

Development of Embryo Sporophyte.—The fertilized egg (zygote or oospore) becomes by repeated division a multicellular embryo sporophyte. In wheat, the zygote undergoes division into two cells a few hours after fertilization. This two-celled body is the **pro-embryo.** The larger cell of the pro-embryo is the suspensor, and from the smaller cell the embryo develops. A depression appears at one side of the **embryo,** marking the position of the growing point of the stem. The scutellum (single cotyledon) arises from the tissue above this depression. The origin and development of the other organs of the embryo are shown in Fig. 404.

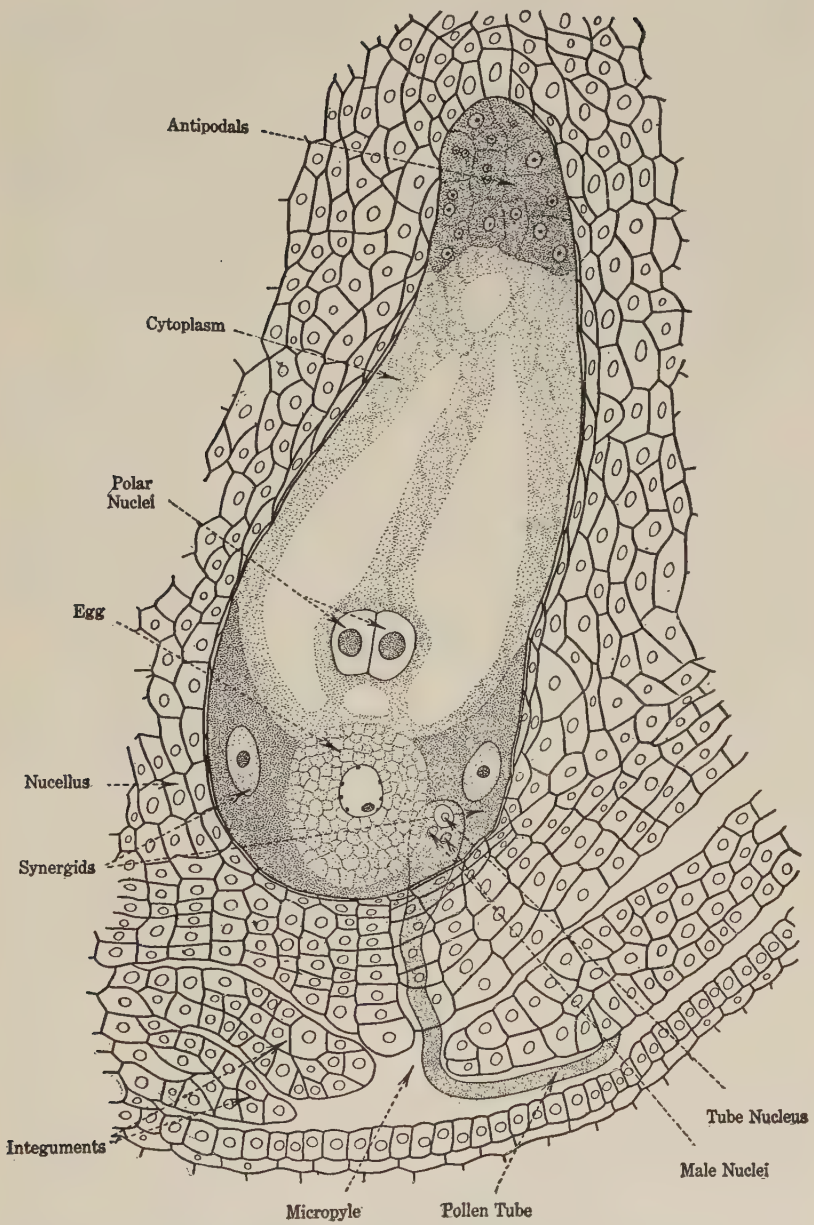


FIG. 399.—Longitudinal section of a mature embryo sac of corn (*Zea mays*) just prior to fertilization. (Redrawn from Miller, in *Journal of Agricultural Research*.)

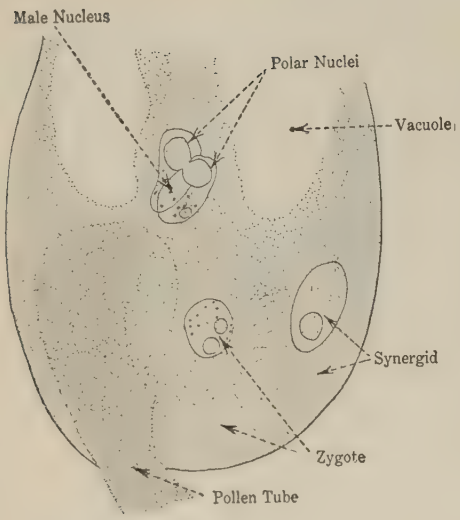


FIG. 400.—Longitudinal section of the lower portion of the embryo sac of corn at the time of fertilization. One male nucleus is shown fusing with the two polar nuclei, and the other male nucleus is shown fusing with the egg nucleus. (Redrawn from Miller, in the *Journal of Agricultural Research.*)

embryo deep down into the endosperm, where each develops into an embryo.

Development of the Endosperm.—It will be recalled that in *Pinus* and in most other gymnosperms the nutritive tissue of the seed, the endosperm, is the female gametophyte, a mass of tissue developed by repeated divisions of the megaspore nucleus. Even at the time of fertilization, this gametophyte tissue makes up a considerable part of the ovule, and after fertilization it continues to grow until it finally displaces all the tissue of the nucellus (megasporangium). In wheat and all other angiosperms, the endosperm has an entirely differ-

It will be observed that in wheat the growing point has a lateral origin, and the cotyledon is terminal in origin. This type of embryo development contrasts with that found in most dicotyledons, as illustrated by *Capsella* in which the growing point is terminal in origin, and the cotyledons are lateral in origin.

In a comparison of the angiosperm embryo with that of the gymnosperm, pine, it is noted that in the latter the pro-embryo consists of a group of sixteen cells, in which the suspensor becomes a much elongated structure pushing four cells of the pro-

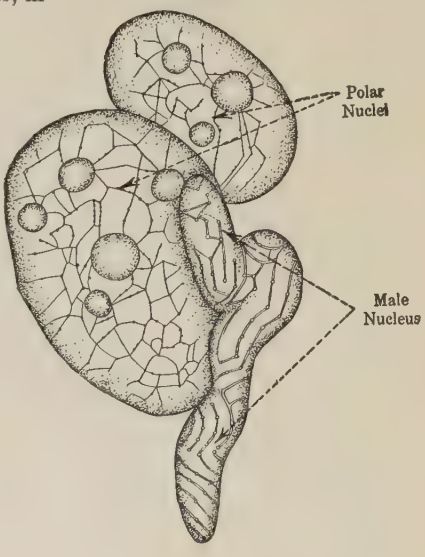


FIG. 401.—Fusion of male nucleus with two polar nuclei, in *Lilium aurantum*, to form the primary endosperm nucleus, ×1260. (Redrawn from Blackman and Welsford.)

ent origin. It is initiated, not by the germination of the megaspore as in *Pinus*, but by the division of the primary endosperm nucleus of the fertilized embryo sac. This nucleus, it will be recalled, is the product of the fusion of three haploid nuclei (two polar nuclei and a sperm nucleus) and accordingly the endosperm is in most angiosperms neither sporophytic (diploid or $2x$) nor gametophytic (haploid or x) tissue, but triploid ($3\ X$) tissue.

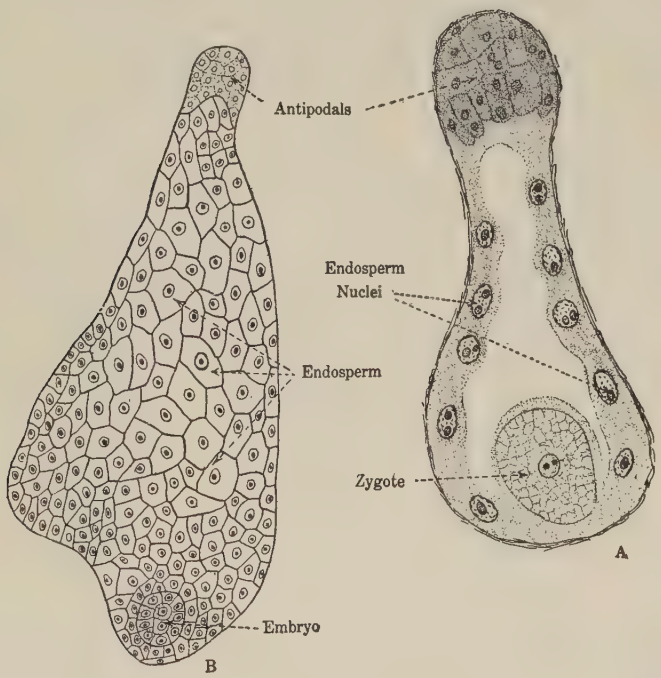


FIG. 402.—*A*, longitudinal section of the embryo sac of corn 12 hours after fertilization. *B*, 36 hours after fertilization. (After Miller, in *Journal of Agricultural Research*.)

Although the first division of the zygote is followed by wall formation and all the cells of the embryo are enclosed in cell walls, the endosperm develops at first by free nuclear division. This phenomenon of repeated division of nuclei without cell wall formation has already been met with in the development of the female gametophyte of *Selaginella*. In wheat, walls are later formed about the free nuclei, and a more or less compact endosperm tissue results, the cells of which are largely filled with starch and protein.

It will be recalled that in many plants, such as peas, beans, alfalfa, squash, sunflower and many others, the endosperm is completely

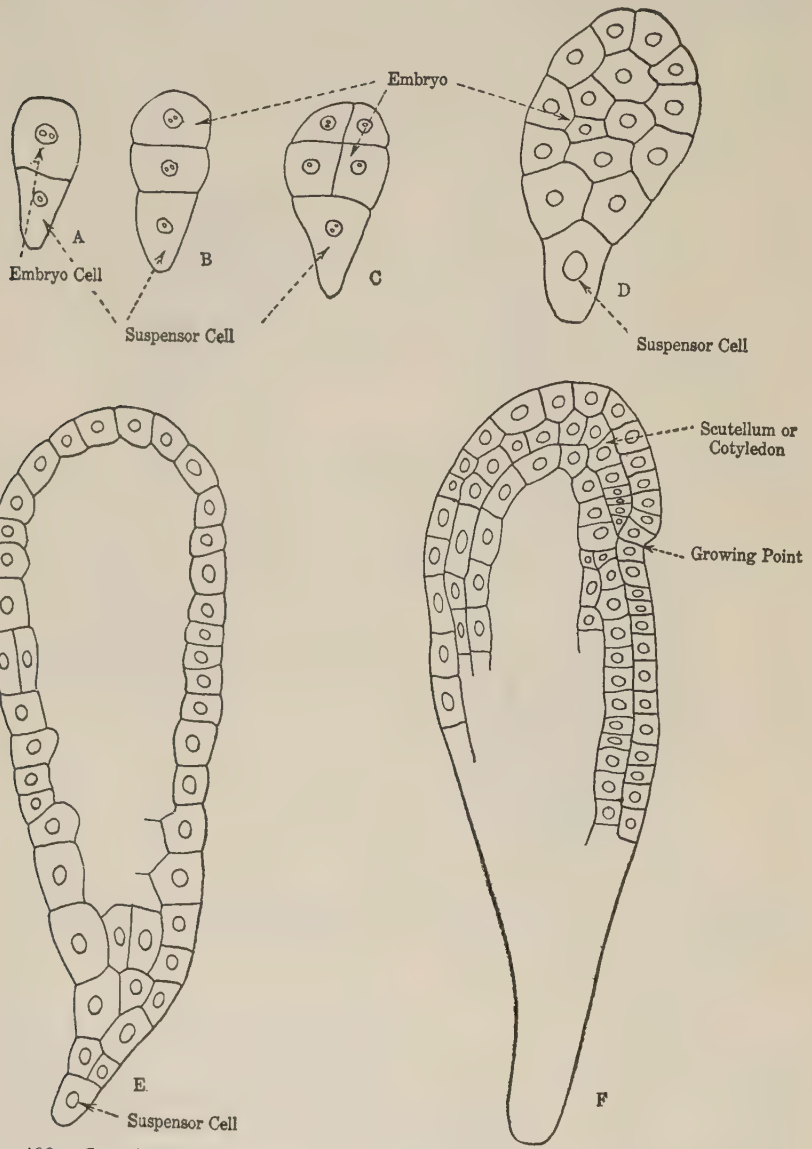


FIG. 403.—Longitudinal sections of young embryos of wheat. In *E* and *F*, some of the cells have been omitted. (Redrawn from Percival.)

absent in the mature seed due to its absorption by the developing embryo. In wheat, as in all other grasses, and in the castor-oil plant,

and many other angiosperms, the endosperm constitutes a large part of the mature seed, performing its function of supplying food to the embryo after germination begins, not before the seed matures.

The Seed.—The development of the angiosperm seed was discussed at length on pages 264–266. The student is referred to those pages in order to refresh his knowledge of this process, which, as described there, is very similar in its essential features to that which takes place in wheat. In the enlargement of the embryo and endosperm, the tissue of the nucellus is encroached upon and either partly or totally absorbed. In the mature wheat seed, the nucellus constitutes a thin layer of cells, covering the outer surface of the endo-

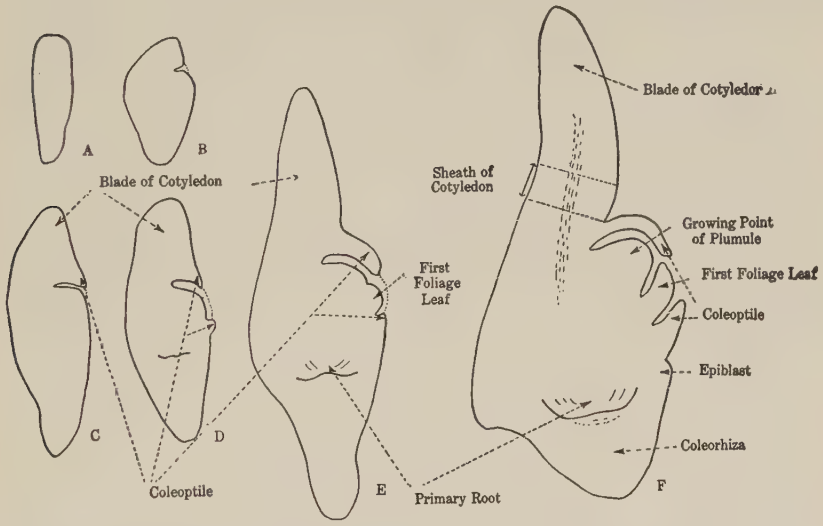


FIG. 404.—Longitudinal sections of embryos of wheat in various stages of development. (Redrawn from Percival.)

sperm. In the young wheat seed, there are two integuments of two layers of cells each. In the maturing of the seed, the outer integument is entirely absorbed, so that the mature seed consists of two rows of cells belonging to the inner integument. It will be recalled that the so-called " seed " or grain of wheat is in reality a one-seeded fruit, in which the ovary wall has become firmly attached to the ovule.

Thus, it is seen that as a result of nuclear fusions in the embryo sac, which is embedded in the megasporangium (nucellus) of the ovule, there follows a series of changes, involving all tissues of the ovule, which result in a structure termed the seed. The mature wheat seed possesses tissue belonging to (1) **the parent sporophyte,** (2) **the embryo sporo-**

phyte, and (3) also an endosperm of triploid origin, which can not properly be designated either as sporophytic or gametophytic. The seed coats and the nucellus belong to the parent sporophyte.

Polyembryony (more than one viable embryo in a seed) in angiosperms has been observed in a number of genera, and arises in various ways. The extra embryos may develop by proliferation of nucellar cells (*Citrus*), from cells of the integument (*Allium odorum*), from synergids (*Taraxacum officinale* and others), and in a number of other ways.

SUMMARY OF THE PRINCIPAL FEATURES IN THE LIFE HISTORY OF WHEAT

1. Formation of the microspore mother cells within the microsporangium (pollen chamber) borne upon the microsporophyll (stamen).

2. Formation of a tetrad of microspores from each microspore mother cell by two successive divisions, of which the first is a reduction division and marks the beginning of the gametophyte generation.

3. Germination of the microspore within the microsporangium (pollen chamber), to form the male gametophyte, which at the time of shedding of the pollen grain consists of two sperm nuclei and a tube nucleus, together with some cytoplasm.

4. Differentiation within the megasporangium (nucellus) of the ovule, of a single megaspore mother cell.

5. Division of the megaspore mother cell to form a row of four megaspores, the first division being a reduction division and marking the beginning of the gametophyte generation. But one of these megaspores develops, and at the expense of the other three.

6. Germination of the megaspore, which by three successive divisions gives rise to eight free nuclei: one egg nucleus, two polar nuclei, two synergids and three antipodals. The antipodal nuclei undergo further divisions giving rise to six to ten nuclei. The mature female gametophyte then consists of from eleven to fifteen nuclei, with accompanying cytoplasm.

7. Escape of the pollen grains (microspores with contained male gametophytes) and their dissemination by the wind. Adherence of pollen grains to stigma of pistil.

8. Further development of the male gametophyte and growth of the pollen tube, through the stigmatic and stylar tissue to the micropyle of the ovule, its penetration of the nucellus and embryo, and discharge of the tube nucleus and two sperm nuclei into the embryo sac.

9. Union of one sperm nucleus with the egg nucleus. The resulting

zygote is the beginning of the sporophytic generation. **Union of other sperm nucleus with two polar nuclei.** The resulting triple-fusion nucleus develops into endosperm.

10. **Development of the embryo sporophyte** by repeated division of the zygote. In this development a pro-embryo is formed, consisting

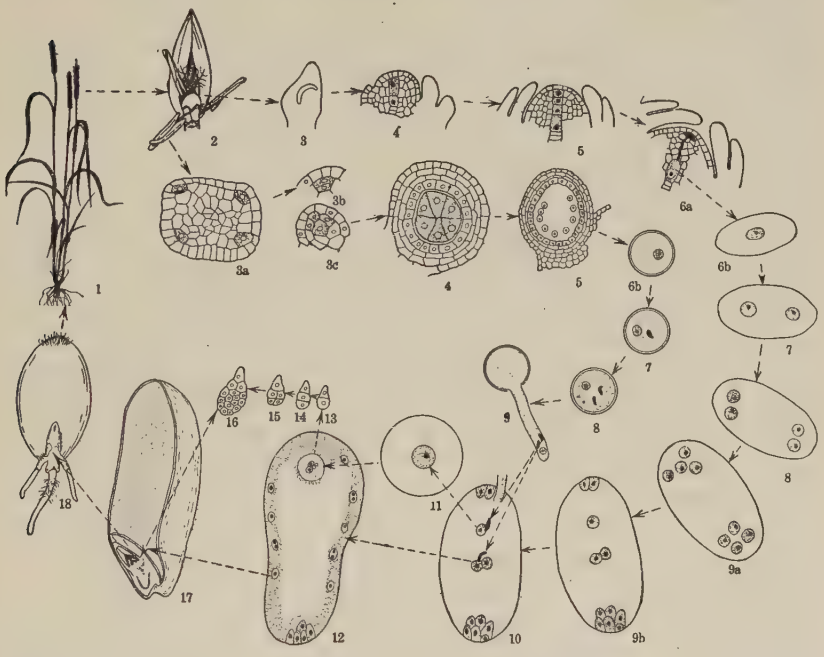


FIG. 405.—Diagrams showing stages in the life cycle of wheat. 1, mature sporophyte; 2, single flower; (outer circle) 3, 4, 5 and 6*a* and 6*b*, stages in the development of the megaspore; (inner circle), 3*a*, 3*b*, 3*c*, 4, 5, and 6*b*, stages in the development of the microspore; (outer circle), 7, 8, 9*a* and 9*b*, stages in the development of the female gametophyte; (inner circle), 7, 8 and 9, development of the male gametophyte and germination of pollen grain; 10, process of double fertilization; 11, zygote; 12, developing zygote and endosperm within the embryo sac; 13, 14, 15, 16, early stages in the development of the embryo sporophyte; 17, mature grain in longitudinal section showing mature embryo and endosperm (dotted); 18, germinating embryo.

of a suspensor and a terminal cell. From the latter the embryo proper develops.

11. **Development of the endosperm** by the free nuclear division of the triple-fusion nucleus, followed by wall formation and subsequent growth.

12. **Development of the ovule into a seed,** involving growth of the embryo and the endosperm, almost complete disappearance of the nucellus, and changes in the inner integuments to form the seed coat.

13. **Germination of the seed.**

14. **Growth into a mature sporophyte plant.**

Important Points of Contrast between Gymnosperms and Angiosperms.—

1. The seeds of gymnosperms are borne upon the surface of the megasporophyll, while the seeds of angiosperms are always formed within a closed structure, the ovary, formed by the union of the margins of one or more megasporophylls.

2. Gymnosperms are all woody, perennial forms, and with few exceptions are evergreen. Angiosperms include both herbaceous and woody plants, and annual, biennial, and perennial forms.

3. In almost all angiosperms, the xylem has tracheal tubes; in all gymnosperms, except the *Gnetales*, tracheal tubes are lacking.

4. In gymnosperms, the pollen comes into direct contact with the megasporangium (nucellus), whereas in angiosperms the pollen comes in contact with the tip of a structure, the pistil (consisting of one or more megasporophylls or carpels), which is developed by and is directly connected with the megasporangium.

5. In contrast to gymnosperms, angiosperms usually have sepals and petals associated with the megasporophylls and microsporophylls, the whole forming a characteristic structure called the flower.

6. In gymnosperms, the first divisions of the zygote result in a number of free nuclei; in angiosperms such free nuclear division does not occur.

7. The male gametophyte of gymnosperms consists of six cells, whereas that of angiosperms is somewhat more reduced, consisting of but three cells.

8. The female gametophyte of gymnosperms is an extensive tissue consisting of many thousands of cells separated by walls and giving rise to archegonia. The female gametophyte of angiosperms is usually an eight nucleate structure (embryo sac), generally without separating cell walls, which never develops archegonia.

9. The more primitive gymnosperms produce motile male gametes; such gametes are not formed in any angiosperms.

10. In the gymnosperm embryo there are generally three to eight cotyledons; in angiosperms either one (monocotyledons) or two (dicotyledons) is the rule.

11. In the angiosperms, the endosperm arises from a triple-fusion cell, and its nuclei, therefore, contains $3x$ chromosomes. In gymno-

sperms there is no counterpart to this tissue, the endosperm of gymnosperms being female gametophyte, and therefore x tissue.

Evolution among the Angiosperms.—There are approximately 125,000 species of flowering plants (Angiosperms) in about 8000 genera and 285 families. Flowering plants are the predominant vascular plants in the world to-day. In the group as a whole there is much variation in the degree of specialization, as concerns both vegetative and reproductive structures, but this is particularly noticeable in the case of the flowers.

We have seen that the angiosperm flower has as its morphological forerunner the strobilus of the pteridophytes. In fact the angiosperm flower has been quite appropriately defined as a "shoot beset with sporophylls." It is quite generally believed that the primitive floral type is that one which most nearly approaches in its structure the strobilus. In such a type of flower we should expect (1) **an elongated floral axis,** (2) **all, or at least some, of the flower parts spirally arranged,** and (3) **stamens** (microsporophylls) **and carpels** (megasporophylls) **numerous and separate.** This combination of characteristics occurs in the buttercups (*Ranunculus*), representatives of the Crowfoot Family (*Ranunculaceae*). For these and other reasons these plants are regarded as being primitive angiosperms, from which the other groups of flowering plants have probably evolved.

The principal tendencies in the evolution of the flower from the primitive type of the buttercup flower are:

1. **From a spiral arrangement of flower parts to a cyclic arrangement of flower parts.** Plants with the spiral arrangement are considered to be more primitive than those with the cyclic arrangement, and there is little doubt that the plants bearing cyclic flowers have evolved from ancestors with flower parts spirally arranged. Thus (among plants belonging to the *Ranunculaceae* or closely related families) the white water lily (*Nymphaea alba*) has its petals and stamens spirally arranged; in the magnolia the carpels are spirally attached, and the buttercup has both stamens and carpels spirally disposed. In most angiosperms, however, the flower parts are arranged in whorls or circles, not spirally.

2. **From a condition in which the ovary is superior** (hypogyny) **to a condition in which it is half-superior** (perigyny) **or inferior** (epigyny). Hypogyny occurs in the buttercups, pinks (*Caryophyllaceae*), mustards (*Cruciferae*), and many other relatively primitive forms; perigyny is well illustrated by the plum and cherry, and epigyny by the orchids (*Orchidaceae*), the honeysuckles (*Caprifoliaceae*), and the asters (*Compositae*).

3. **From a condition** (apocarpy) **in which the carpels are separate** (each of the several pistils consisting of a single carpel) **to a condition**

(syncarpy) **in which the carpels are united.** The compound pistil is regarded as the more advanced type. The buttercups, water lilies, and magnolias are good examples of apocarpous flowers, whereas most flowering plants have, like the lilies, primroses, gentians (*Gentianaceae*), and mints (*Labiatae*), syncarpous flowers.

4. **From a condition in which the petals are lacking** (apetaly) **or, if present, separate** (polypetaly) **to one in which the petals are united** (sympetaly). The willows (*Salix*), buckwheat, and beet are a few of the many plants in the apetalous families; the rose, apple, and mustard belong to polypetalous families, and the mints, morning glories, and potato are examples of plants with sympetalous flowers.

5. **From a condition of radial symmetry** (actinomorphy) **of the flower,** as in the lily, rose, and morning glory, **to bilateral symmetry** (zygomorphy), as in the snapdragons (*Scrophulariaceae*), orchids, and mints. Zygomorphic flowers are presumably an adaptation to insect visitation, facilitating cross pollination, and it appears that plants with such flowers were evolved from plants with actinomorphic flowers.

6. **From a pentacyclic condition** (with five whorls of flower parts) **to a tetracyclic condition** (with four whorls of flower parts), or to **still further reduction of floral whorls.** For example, in the primroses (*Primulaceae*), there are five sepals, five petals, two whorls of stamens of five each, and five carpels (united), thus making five whorls or cycles. The flowers of the gentians (*Gentianaceae*), morning glories (*Convolvulaceae*), and phloxes (*Polemoniaceae*) on the other hand, are tetracyclic, having only four whorls, the arrangement being in general five sepals, five petals, five stamens, and two carpels (united into a single pistil).

PRINCIPAL TENDENCIES IN THE EVOLUTION OF THE FLOWER

As already stated, the buttercup flower may be regarded as the primitive type of angiosperm flower. In it there is a combination of the following primitive characteristics: **spiral arrangement of stamens and carpels, indefinite number of stamens and carpels, actinomorphy, no elevation of the corolla or other whorls relative to the carpels.**

From this primitive type of flower there seem to have been at least three main lines of advance. These three lines culminated in forms represented respectively by the **orchids** (*Orchidaceae*), the **mints** (*Labiatae*), and the **asters** (*Compositae*). In these three families there is a combination of advanced characteristics, namely: **cyclic arrangement of flower parts, a definite number of stamens and carpels, zygomorphy, both coalescence and adnation of flower parts, and an elevation of the corolla** (the ovary being inferior).

Intermediate between the buttercup type of flower and the flower type of each of these three families are the flowers of other families of angiosperms showing various degrees of advancement above the primitive buttercup type.

Figure 406 [1] shows diagrammatically the three principal lines of evolution of flower type as illustrated by a few important angiosperm families. One of these lines of descent passes through the lilies (*Liliaceae*) and the irises (*Iridaceae*) to the orchids, a second through the roses (*Rosaceae*), saxifrages (*Saxifragaceae*), and honeysuckles (*Caprifoliaceae*) to the asters, and the third through the geraniums (*Geraniaceae*) and phloxes (*Polemoniaceae*) to the mints.

For an understanding of this diagram it is essential to know the number and arrangement of the parts of the flowers of each of the families mentioned. This information is supplied by the flower "formula" given below the common name in each case. In these formulae Ca stands for sepals, Co for petals, S for stamens, and P for carpels. Figures (exponents) placed after the symbols for any flower part indicate how many such parts are found in the flower, ∞ standing for "numerous." Parentheses enclosing an exponent means that the parts in question are more or less coalesced (united). When all the symbols are written in a single line, as in buttercups, lilies, and geraniums, it indicates that none of the parts are raised above others. When certain of the symbols are written above certain others it indicates that the upper ones are raised above the others in the flower. When the exponents are written thus, $Co^{(5+0)}$, or $Ca^{(3+2)}$, instead of merely Co^5 or Ca^5, the flower is zygomorphic (not actinomorphic or star-shaped).

The floral formula for the buttercups indicates that there are 5 to 15 calyx segments (Ca), 0 to 5 corolla segments (Co), numerous (∞) stamens (S), and numerous (∞) carpels (P); moreover, there is no union of flower parts as is indicated by the absence of parentheses around the exponents 5-15 or 0–15, and there is no elevation of parts, as is shown by the writing of the four symbols in a line. It is seen from the chart that the typical rose type of flower (family *Rosaceae*) has essentially the same structure as that of the buttercup, except that in roses the corolla segments and stamens are elevated, that is, are inserted on the margin of a disk which is an outgrowth of the receptacle. This elevation of the petals and stamens is shown in the floral formula by writing their symbols (Co^5S^∞) above a line, below which is $Ca^5P^{1-\infty}$.

The rose-saxifrage line of advance culminates in the asters (family

[1] The chart method of showing family relationships was originated by F. E. Clements, on the basis of the Besseyan system. Reference is made here to Clements and Clements Rocky Mountain Flowers.

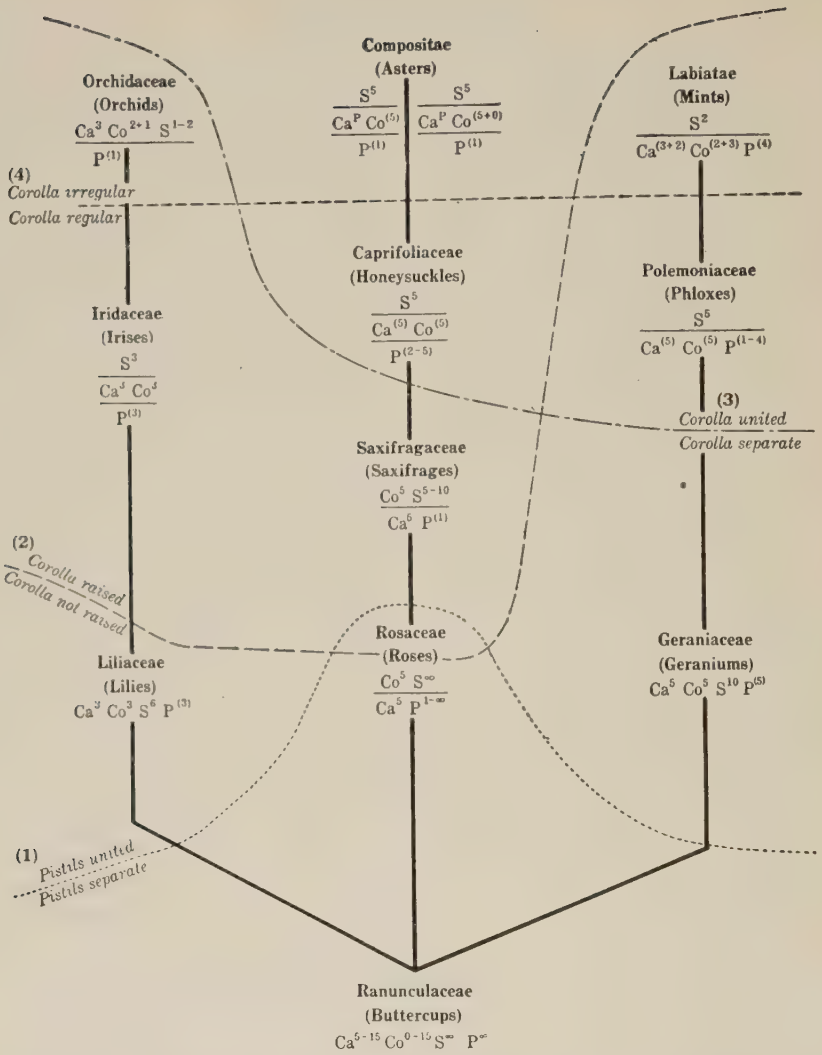


FIG. 406.—Chart showing the principal lines of descent and tendencies in the evolution of angiosperm flowers. In the flower formulæ, Ca stands for sepals, Co for petals, S for stamens and P for carpels. The exponents give the number of the flower parts in the different whorls. Parentheses enclosing exponents indicate that the flower parts of the whorl in question are more or less united with each other (coalescent). When there are two exponents for a single whorl with a plus sign between them the flower parts are in two groups, as in the Labiatae where the corolla is two-lipped, one lip consisting of two petals, the other of three. When the symbols for certain flower parts are separated from others by a horizontal line those above the line are raised in the flower above those below the line.

The position of any family in the chart and its flower formula do not in all cases hold for all the genera and species of the family but are characteristic of the family as a whole.

Compositae), the flowers of which were described on page 257. The second dicotyledonous branch from the buttercups includes, among others, the geraniums (family *Geraniaceae*) and phloxes (family *Polemoniaceae*) and culminates in the mints (family *Labiatae*). The principal tendencies in the evolution of the flower are also shown in this branch, except that there has been an elevation of the stamens only, the corolla not being raised (i.e., the flowers are hypogynous). In the formula for the *Labiatae*, $Ca^{(3+2)}$ indicates that the calyx is 2-lipped with 3 lobes in one lip and 2 lobes in the other, and the parentheses about the exponents indicate the union of calyx segments; likewise $Co^{(2+3)}$ indicates a 5-toothed sympetalous 2-lipped corolla. In the monocotyledonous branch, from the buttercups, through lilies (family *Liliaceae*), irises (*Iridaceae*), to orchids (*Orchidaceae*), there has been a reduction in the number of parts in each floral whorl to 3, which is characteristic of most monocotyledonous flowers.

Orchid flowers are noted for their pronounced zygomorphy, which character contributes to their peculiar beauty and grotesqueness. The perianth is composed of two whorls of three members each. The three segments of the outer whorl (sepals) are usually similar in shape and texture, but one member of the inner whorl (petals) is highly modified to form a prominent lip and spur, or a peculiar sac or pouch. In the ancestors of present-day orchids the stamens were six in number, but in most extant orchids there is but one functional stamen. The ovary consists of three united carpels and is inferior, all the other parts being raised above it.

The chart shows that, in each of the three lines of development there are four tendencies in the evolution of the flower; namely, (1) from pistils separate to pistils united; (2) from corolla not raised to corolla raised; (3) from corolla separate to corolla united and (4) from corolla regular to corolla irregular. Although this chart shows but a few angiosperm families, it may be used to ascertain roughly the position and relationship of the families. For example, examination of the flower of a typical reprsentative of the potato family (*Solanaceae*), shows it to have 5 united sepals, 5 united petals, 5 stamens inserted on the corolla, and 2 carpels united into a single pistil. Its floral formula is therefore, $\frac{S^5}{Ca^{(5)}Co^{(5)}P^{(2)}}$. Examination of the chart indicates that this family is quite closely allied with the phloxes (*Polemoniaceae*).

In Figure 407 a more complete chart is given, showing many more families and showing, in each of the three lines of descent, two main branches: one made up of insect pollinated families with conspicuous flowers and one of wind pollinated flowers. The wind pollinated

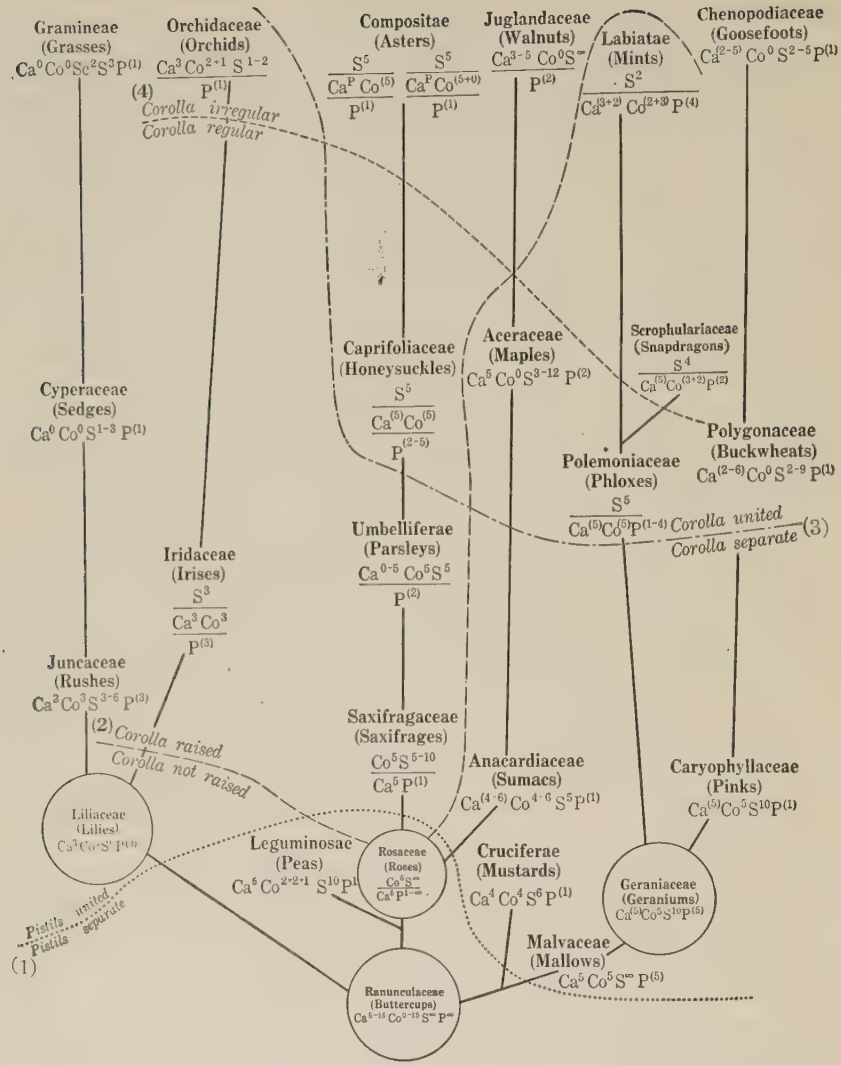


FIG. 407.—Chart showing the principal lines of descent and tendencies in the evolution of flowers in the angiosperms and the relationships of twenty-five important families. Each of the three principal lines of descent represented in Fig. 406 are here shown to consist of two more or less parallel lines, one made up of insect-pollinated, the other of wind-pollinated plants. Thus, of the two series having their origin in the Liliaceae the one culminating in the Graminae consists of wind-pollinated plants, that ending in the Orchidaceae of insect-pollinated plants. Similarly the two series leading up to the Compositae and the Labiatae are made up of plants mostly pollinated by insects and the Juglandaceae and the Chenopodiaceae lines are wind-pollinated. This and the simpler chart (Fig. 406) are adapted from charts by Clements and Clements in *Rocky Mountain Flowers* and other publications.

series ends, in the lily line, with the grass family, in the rose line with the walnuts (*Juglandaceae*) and in the geranium line with the goosefoots (*Chenopodiaceae*).

The chart may be used to ascertain the family to which a flowering plant belongs or at least to determine quite closely what are the relationships of the family to which it belongs to other families and thus greatly simplify the working out of its genus and species. In using the chart for this purpose it is first of all essential that the floral formula of the flower of the plant in question be carefully worked out. "The steps of advance which affect the pistil must be the first to be considered in 'placing' the flower in its proper place.[1] Of these steps affecting the pistil the union of simple pistils into a compound one must be considered first of all and then the elevation of the corolla on the ovary, second. The other two changes affect the corolla also, and of these the uniting of the petals into a bell or tube is of the most importance and should be considered next. The change in shape of the corolla (corolla regular to corolla irregular) is of the least weight in determining flower relationships. This is because irregularity of corolla, though characteristic, of all of the highest groups may occur occasionally in almost any group, even the buttercups. For this reason, the steps of advance must be followed in the order in which they occur across any of the three lines of development and no one can be 'skipped' in order to reach a farther one. Since the ovary is the keynote to the family relationships, one must be very careful to determine with certainty whether it is simple or compound, and if the latter, exactly how many cells it possesses. This must be done by a cross-section of as mature an ovary as possible, and determined not from one specimen but from several. It is well to study the other parts from several specimens also, as variations from the normal may occur in any one and so spoil results."

Distinctions between Monocotyledons and Dicotyledons.—In the use of the chart method, or any other method, for the determination of the family to which a plant belongs, the student should bear in mind the important differences between the two classes of the angiosperms; they are briefly:

1. The leaves of monocotyledons are generally parallel-veined and almost always have entire margins whereas the leaves of dicotyledons are generally net-veined and are very frequently toothed, lobed or compound.

2. With few exceptions the number of flower parts of any one kind,

[1] This sentence and the remainder of the paragraph are quoted from the instructions for the use of the chart for plant determination in Clements and Clements, *Rocky Mountain Flowers*.

i.e., carpels, stamens, petals or sepals, is three or some multiple of three in the monocotyledons. In the dicotyledons it is generally four or five or some multiple of four or five.

3. In the stems of monocotyledons the conducting tissue is in numerous vascular bundles scattered through the stem but not arranged in a single ring. Dicotyledonous stems have the conducting or vascular tissue either in a hollow cylinder surrounding the pith and increasing in width as the stem grows older or distributed in separate bundles arranged in a single circle.

4. The embryos of the seeds of monocotyledons have only one cotyledon or seed leaf whereas in the dicotyledonous embryos there are generally two cotyledons.

In the first chart (Fig. 406) monocotyledonous families are shown on the line of descent which is furthest to the left. In the chart in Figure 407 they are on the " wind-pollinated " line culminating in the *Graminæ* and the " insect-pollinated " line leading up to the *Orchidaceæ*.

CHAPTER XVI

EVOLUTION AND HEREDITY

Evolution.—The evolution of plants and animals is a subject of very great popular and scientific interest. In discussions of the subject, however, there has frequently been confusion of two quite different things: the fact of evolution and the means by which it is brought about. It has long been held by those best acquainted with plants and animals that all the thousands of species of plants and animals which exist to-day, or have existed in the past, have originated from previously existing species and that they all therefore have arisen by the process we call evolution from one or a few original kinds. Although it is one of the principles of scientific thinking that such a theory as that of evolution is to be accepted as true only in the sense that it is highly probable, it can safely be said that no biological theory is better substantiated by the evidence than that of organic evolution. To accept evolution as a fact does not necessarily involve the endorsement of Darwin's theory of how evolution has been and is being brought about, or of any other particular theory as to the method of evolution. At the same time, this problem of how new species evolve must be recognized as one of the most important of all problems having to do with living things.

Accepting the fact of evolution, we shall attempt in this chapter to summarize, in so far as is possible in a few pages, the principal theories as to the method of evolution and some of the most important facts bearing upon these theories.

Heredity and Variation.—It is inconceivable that the many species of plants and animals which exist about us could have evolved but for two remarkable tendencies which are characteristic of all organisms. These two tendencies are **heredity** and **variation**. Heredity may be defined as the tendency of the progeny to be like the parents and therefore to resemble each other. Heredity is a conservative tendency, in the absence of which there could be no such things as species, for a species is a group of very similar individuals related by descent. Variation, on the other hand, is the tendency of the progeny to differ from the parents and therefore from each other. It is clear that without variation no new species could ever have arisen from pre-existing species.

That like begets like is one of the most obvious facts in human experience. Even primitive peoples recognize the fact that characteristics are passed on from parents to children and that acorns, the seed of oaks, always grow into oaks and never into pines or apple trees. In fact this similarity between parents and progeny is so obvious, at least among organisms other than human beings, that it is commonly assumed to be much more complete than it really is and only the most conspicuous differences are recognized at all.

It is among the individuals of our own species that the non-conservative tendency (variation) is most obvious, at least to those who are not students of heredity. Except in the case of some twins having unusually close resemblance, there is always sufficient variation among the children of a single family, aside from differences in age and sex, to make it easy to distinguish them from one another. Moreover, in the rare cases where two individuals of the same or different families show very close likeness, it is only necessary to employ fairly accurate methods of measurement to show that many differences exist between such individuals. Thus it is literally true that no two individuals of our species are exactly alike. The familiar expression " as like as two peas in a pod " which is so commonly used to indicate the closest of resemblances, directs the attention of the individual to an excellent example of the dissimilarity (variation) which we find among all plants and animals, for actually no two peas are alike. In fact, every pea in a pod, and even every pea on a plant is different from every other, and the plants which would develop from these peas, if they germinated, would all show differences in such particulars (characters) as size and form of the root system and of the shoot, branching, form, size and arrangement of the leaves, size and arrangement of the flowers, and many other characters.

There immediately suggests itself, in connection with heredity and variation, the question of the actual cause of these tendencies. Why do the progeny tend to be like the parents and why are they often quite unlike and always slightly different from the parents? The cause can be stated more briefly and simply in the case of heredity than in that of variation. The progeny generally closely resemble the parents because their living substance is derived from the parents. If the new individuals have arisen by vegetative methods, as in the case of stem cuttings and bulb formation, it is clear that all the protoplasm of the new plant came originally from the single parent. In sexual reproduction the new individual develops from a fusion cell or zygote in which are combined a protoplast from one parent with a protoplast, or at least a nucleus, from the other parent. In either case there

is continuity of living material from parent to progeny and the tendency to likeness must be due to this continuity. The fact that in many seed plants only the nucleus, and apparently none of the cytoplasm, of the male gamete, fuses with the egg cell, indicates that at least in these cases it is the nuclei which make possible the reappearance of parental characters among the offspring.

Chromosome Theory of Inheritance.—Within recent years a great deal of study has been devoted to the subject of the relation of the nucleus to inheritance. Out of this study has grown the chromosome theory of inheritance, according to which the chromatin of the chromatin granules of the resting nuclei and of the chromosomes of dividing nuclei bear the inherited characters. It will be recalled that the number of chromosomes is constant for each species, except, of course, for the fact that the number is doubled at fertilization and halved again at the reduction division. There is very good reason to believe that the identity of these chromosomes is not lost in the period between nuclear divisions, even when they break up into chromatin granules and remain in that condition in the resting nucleus. In fact there is little doubt that each chromosome which a daughter nucleus receives in the anaphase of one mitosis is reconstituted in the prophase of the next. It has been shown very conclusively in a few organisms, and it is probably true in all, that each of the chromosomes of a haploid nucleus is the bearer of a different group of inherited elements. It is also very probable that each chromosome is actually made up of a linear series of elements, genes, each of which is concerned in the development of one or several characters. It follows, then, that the chromosomes of a haploid nucleus all differ in the character-conditioning units which they carry.

In the diploid nucleus, on the other hand, there are two chromosomes which condition the same group of characters. One of these we shall call the maternal and the other the paternal chromosome, since they were contributed respectively by the female and the male gamete when the zygote was formed at fertilization. Since the chromosomes correspond in the characters which they condition and in the order in which the genes or hereditary units are arranged, they are called **homologous chromosomes** (Fig. 412). Each of the pairs of chromosomes which appear at the reduction division consists of two homologous chromosomes which have become separated from each other at the metaphase. Accordingly, each of the daughter nuclei, resulting from the reduction division, *contains one from each pair* of homologous chromosomes but *does not contain any pair* of homologous chromosomes. It contains one chromosome for each group of characters, but only one instead of two as do the diploid nuclei. It follows, therefore, that the nuclei of the mega-

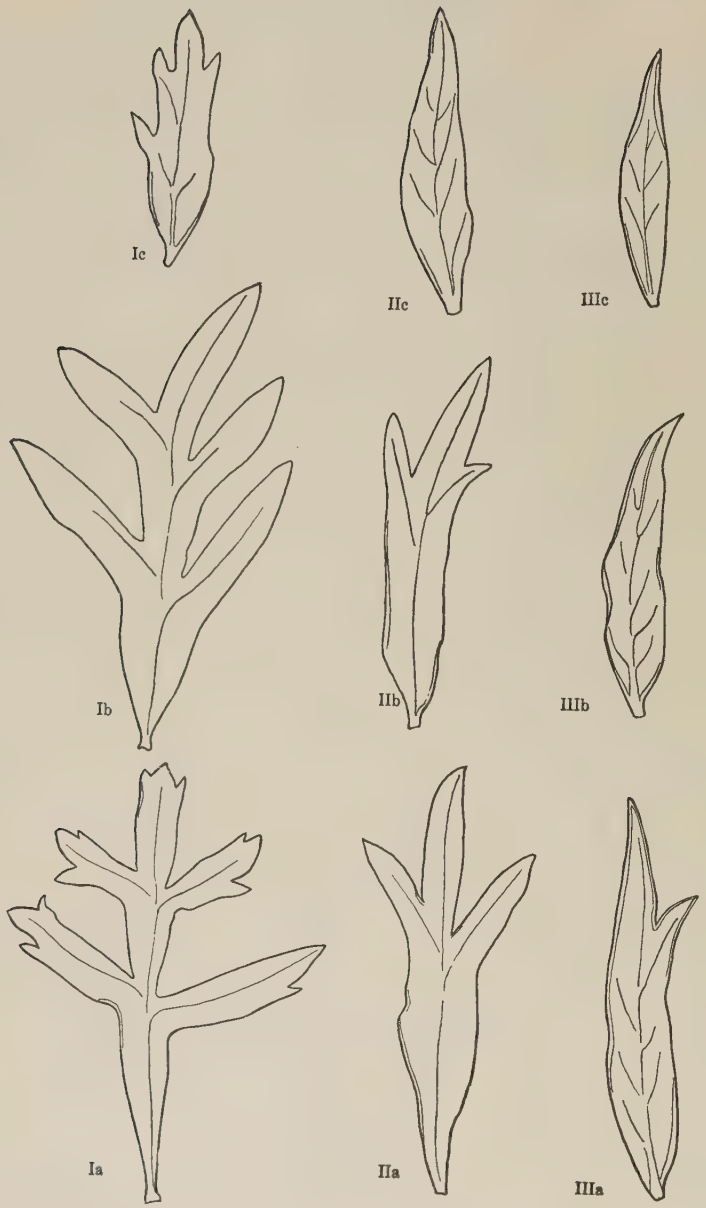


FIG. 408.—Leaf variations in *Artemisia vulgaris*. The leaves in each vertical row are from a single plant and thus show variation in one individual. Thus 1*a* is from near the base of a given plant, 1*b* from about half way up the stem of that plant and 1*c* from near the tip of the same plant. The leaves in each horizontal row are from corresponding parts of three different plants and thus show variations between different individuals. (Redrawn from Clements and Hall's *The Phylogenetic Method in Taxonomy*.)

spores and microspores of the seed-bearing plants, and the nuclei of the embryo sac and pollen tube including the egg cell and male gamete, likewise contain only a single chromosome for each group of characters. Although there are a few cases in which characters are apparently conditioned by the cytoplasm it is certain that with rare exceptions inheritance is due to the continuity of chromatin from one generation to another.

FIG. 409.—A series of pinnae of various bud mutants of the Boston fern (*Nephrolepis exaltata bostoniensis*), itself a bud mutant. The pinnae shown are: 1, *var. bostoniensis*, the original mutant form, and 2, *Piersoni*; 3, *Whitmani*; 4, *Goodi* (or *gracillima*); 5, *magnifica*; 6, *Craigi*; 7, *Amerpohli*. (From *Genetics in Relation to Agriculture* by Babcock and Clausen, McGraw-Hill Book Co.)

Kinds of Variations.—The differences (variations) which exist between the individuals of a species or race may be conveniently grouped into three kinds:

(1) Modifications
(2) Combinations
(3) Mutations.

Modifications.—Modifications are variations which are not inherited and which are due to differences in the external conditions (environmental factors) to which different individuals are exposed. It is a matter of common observation that plants of the same species, even if grown from seeds of the same plant, may be very unlike when grown in very different habitats. Thus when plants of moist valleys are grown from seed or by transplantation in alpine regions, their internodes are generally shorter, their leaves are smaller and thicker, and their flowers

are larger than when they grow in their natural habitat. If the seeds of these plants are planted in the natural habitat again, it will be found that the modifications which the species displayed when grown in an alpine habitat have not been inherited. Much less conspicuous environmental differences than those which are characteristic of the habitats just mentioned may call forth considerable modifications. This is evident from the great differences which are frequently noticeable between plants of the same variety in different parts of a grain field, and which are due to differences in such environmental factors as soil moisture, soil fertility and illumination. It is probable that these differences in environment do not bring about any change in the chromatin of the plants and therefore are not inherited.

Combinations.—It is known that there are often **heritable** differences of varying degree between the individuals of a species or variety. These may combine in various ways in the progeny of two such individuals, thus giving rise to variations which are spoken of as combinations. Thus when plants of two different species or varieties are crossed (hybridized), as when one variety or species is pollinated with pollen from another, there may be among the progeny some individuals which resemble one parent, some which are like the other parent, and still others which on account of a combination of characters are, in some respects, unlike either of the parents.

Mutations.—Mutations are sudden and sometimes relatively large differences which occasionally make their appearance in a few individuals out of many hundreds or thousands. It is only when such changes appear among individuals which are not of hybrid origin that their occurrence may be attributed with certainty to mutation. The characters arising by mutation are heritable except in the case of certain bud mutations which are shortly to be discussed. This type of variation (mutation) is apparently not due to the combination of different parental characters but to changes in the nuclear material. These changes are of two general categories: (1) an alteration in a single hereditary element, gene, in a particular chromosome; (2) irregularities in the distribution of the chromosomes in cell division so that whole chromosomes or pieces of chromosomes are lost from or added to the normal chromosome complement. Mutations occur not only from plants raised from seeds—the so-called seed sports—but may also arise from one or a few of the buds of a normal plant. Such cases are spoken of as bud mutants or bud sports. Some of the most valuable varieties of ornamental and other economic plants have originated as bud mutations. In the case of many, but not necessarily all, bud sports, the seeds produced by the flowers of a sport branch, even though pollinated by

pollen from the same branch, do not give plants having the characteristics of the sport or bud mutant. That is to say, many bud sports do not "breed true," and must be propagated vegetatively by means of cuttings or by some method of grafting.

There are not many familiar varieties of economic plants which can be stated definitely to have had their origin in seed sports. This is in part due to the fact that most of the widely known varieties of economic plants originated long ago, and accordingly little is known as to their origin. To-day, however, plant breeders are constantly on the lookout for such mutations and recognize them as possibly furnishing the material for the production of desirable new varieties. The sweet pea (*Lathyrus odoratus*) is a domesticated plant as to whose history, since the beginning of its culture, we are well informed. A number of new and desirable character differences are known to have originated in seed sports of sweet peas. In the two centuries and over since the sweet pea was first used as a horticultural plant, at least a dozen distinct color mutations have thus arisen, as well as several mutations which involved changes in the size and form of the flowers and in the number of flowers borne upon a flower stalk. By no means all of the many hundred varieties of this plant have, however, arisen as seed mutations. The greater number have arisen by hybridizing or crossing of different varieties which originally arose by mutation.

Among the many varieties of economic plants which have arisen as bud mutants are the copper beech, the numerous variegated kinds of *Coleus*, numerous forms of the Boston fern (*Nephrolepis exaltata bostoniensis*), itself a bud mutant of the tropical *Nephrolepis exaltata*, and a few varieties of oranges, apples, and other fruits. (Figs. 409 and 410.)

Theories as to the Origin of Species.—Having discussed the phenomena of heredity and variation which are fundamental to any explanation of the method of evolution, we shall give a brief account of some of the principal theories of evolution.

Long before Darwin's remarkable studies of the origin of species, which aroused such wide popular and scientific interest in evolution, a number of theories had been advanced as to the method of evolution.

Direct Response to Environment.—According to the theory of Geoffroy St. Hilaire, the French naturalist (1772–1844), new species have arisen in direct response to changes in the environment. That is to say, as climatic and other conditions on the surface of the earth have slowly altered, these changes have directly modified the individuals of certain species and have thus called forth variations. A succession of such variations in a species might result in the production of a new species. St. Hilaire believed some of these changes to have been favorable, or at

least, not unfavorable, and that the individuals which underwent these changes survived. Others were unfavorable and resulted in the destruction of the individuals.

Use and Disuse.—Jean de Lamarck, another French naturalist, proposed an explanation of evolution which is commonly spoken of as the theory of "use and disuse." It is a familiar fact that, in the case of individuals, the continued use of a part of the body, as, for instance, the muscles of the arm of a blacksmith, results in a development of that organ which makes it better able to do the work habitually required of it.

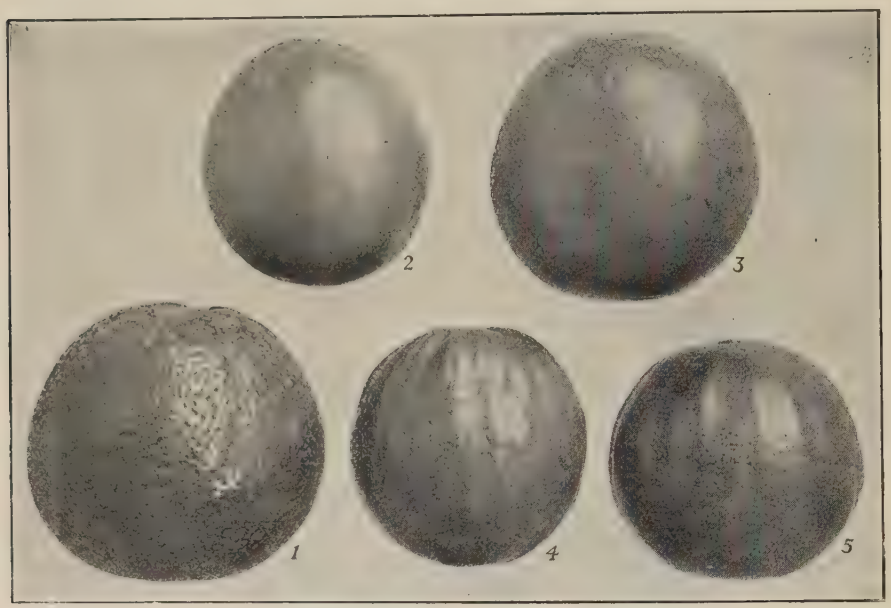


FIG. 410.—Fruits of the Washington navel orange 1, and of four strains that have originated from it by bud variation; 2, Thomson navel; 3, yellow navel; 4, corrugated; 5, ribbed. (From *Genetics in Relation to Agriculture* by Babcock and Clausen, McGraw-Hill Book Co.)

It is also true that persistent disuse of an organ is apt to result in its partial degeneration or even suppression. Now, Lamarck believed that changes in the environment might bring certain organs into disuse and increase the extent to which other organs were used, and thus bring about degeneration of certain organs and build up or modify others. Moreover, and this was the most important feature of his theory, he regarded the characters thus acquired during the life of an individual as heritable. Thus the environment might, by reduction or suppression of certain organs and development of others, cause new species

to arise. Among numerous illustrations of his theory, he used the neck of the giraffe. He assumed that the ancestors of the giraffe were grazing animals with short necks, and that some change in the environment made it necessary or desirable for them to feed upon the leaves of trees. This, he believed, called forth a slight elongation of the neck which was transmitted by the individuals to their progeny. By inheritance and continued use (reaching upward for leaves), the elongation became greater from generation to generation until the remarkably elongated neck of the giraffe had been evolved. Lamarck's theory was founded on three assumptions: (1) that the environment changes, (2) that use and disuse may alter the character of an individual, and (3) that such alterations can be inherited. The first two assumptions are recognized as correct, but there is no convincing evidence to indicate that acquired characters (modifications) can be inherited.

Orthogenesis.—Another theory, which has been advanced by different men and in different forms, is that there is inherent in every species a tendency to vary in a certain definite direction. If variation in this direction does not result in the individuals' becoming less favorably adapted to their environment, new species will arise and these in turn will give rise to others. Otherwise, the variations will not persist. The principal objections to this theory are as follows: (1) It has never been shown that such a persistent tendency to vary in a certain direction does exist. (2) No explanation has ever been given as to the driving force or principle which is responsible for the assumed tendency.

Darwin's Theory of Natural Selection.—The most famous of the theories of evolution is Charles Darwin's theory of natural selection. The principal features of this theory are as follows:

(1) **Plants and animals in nature produce many more progeny than can possibly survive.** Long before Darwin's time it was computed by Linnæus that if an annual plant produced two seeds each year, and each of these, which in turn produced two seeds—and so on, grew into a plant, there would be after twenty years over a million plants. The common shepherd's purse (*Capsella*) may produce upon a single plant as many as 64,000 seeds, and a tobacco plant at least 360,000 seeds annually. There are plant species of which an individual may develop in a single year, 74 or 75 million seeds, and one tropical fern which produces 200 billion spores annually per individual. Actually, a very small proportion of these seeds or spores—in general only a small fraction of one per cent—ever germinate, and only a few of the seedlings grow to maturity.

(2) **On account of this production of individuals far beyond the earth's facilities to support them, there is a struggle for existence.** That

is to say, there is an intense competition in nature for water, light, food, and raw materials. This competition is going on (*a*) between different individuals of the same species, (*b*) between the individuals of one plant species and those of other species of plants, and (*c*) between certain plant species and certain animal species. Darwin found that of 357 seedlings which came up in a cleared piece of land, 3 by 2 feet square, 295 were destroyed, principally by insects.

(3) **Individual organisms or different species differ in their fitness for a given environment.** Clearly, the water lily is not fitted to live in a desert nor the cactus to grow in a pond. Also, among plants living in a given habitat, some are better fitted for that environment than others.

(4) **Through the struggle for existence, there is a natural selection which results in the survival of the fittest, or to put it conversely, in the destruction of the unfit.** Thus nature may be said to determine which individuals will survive and give rise to successive generations.

(5) **The individuals of a species are not all alike and even among the progeny of the same parents there are always at least slight variations** (a fact already discussed earlier in this chapter). Darwin assumed these variations to be heritable. He also believed that by the destruction of the individuals whose variations reduced their fitness, and by the selection for survival and reproduction of those with variations which better fitted them for the environment, the original differences might be increased so that a new species would have its origin.

Darwin collected and published a great mass of data in support of his theory of natural selection, and his publications led many to the acceptance of the theory of organic evolution. Although, at the present time, many biologists do not accept in its entirety his "theory of the origin of species by natural selection," it is certainly true that his work has done more to stimulate workers in the field of biology than that of any other man who has ever lived.

It is now quite generally accepted that natural selection is a most important factor in evolution, but there are a number of serious objections to Darwin's particular theory of evolution by natural selection. We shall discuss briefly some of the most important of these objections. (1) The variations which, according to Darwin, provide the material for natural selection are of the type called **continuous** or **fluctuating variations.** Illustrations of this kind of variation can be secured by measurements of any organ or structure in many individuals of a given species of plant or animal. Thus if the length of all the beans in a lot is measured, and if all those having approximately the same length be sorted out, the

following relation will be found to exist: The number of the beans having the least length will be very few. Those having the greatest length will also be very few. Between these extremes the numbers will increase as we approach the length halfway between the two extremes, at or near which we will find the largest number of individuals. Now it is known that if the variations in question are heritable (and some fluctuating variations can be inherited), it is possible, for instance, by selecting through some generations to increase the average length of the beans. Thus the length characteristic of the greatest number of beans in any generation would be displaced in the direction of the extreme length. There is no reason, however, for believing that the extremes would change. Instead, the greatest length and the shortest length would remain the same, and unless the extremes of variations can be shown to be changed by selection nothing new has been produced. The mere increase in the relative number of individuals varying in a given degree which already existed can not account for the origin of a new species. In short, natural selection of fluctuating variations can not push the range of variation beyond certain boundaries which are characteristic of a species.

(2) Another important objection to Darwin's theory is that the variations upon which Darwin believed natural selection to operate are scarcely of sufficient degree to be of life and death importance, as would be necessary if his theory were correct.

(3) Furthermore, many of the characters which differentiate one species from another can scarcely be conceived of as having anything to do with the fitness for the environment.

(4) It has also been pointed out that by far the greater number of the individuals which succumb in the struggle for existence do so in the very early stages of their development (seedlings and young animals) and thus before many of their characteristic differences have appeared.

The Mutation Theory of Evolution.—Hugo De Vries, the great Dutch student of mutation, has pointed out that the principal objections to Darwin's theory are removed if we abandon the idea that species can be originated by natural selection of minute fluctuating variations. He suggests that new forms originate by mutation rather than by natural selection. The principal features of de Vries' theory of evolution are the following: (1) There arise from time to time, among the individuals of a species, forms which differ relatively widely in one or more characters from typical individuals. (2) The distinguishing characters of these mutant individuals are inherited, at least in many cases. (3) These mutations arise quite independently of fluctuating variations. (4) Mutations may take place in any direction. (5) The mutants (mutat-

ing individuals), at least in many cases, differ sufficiently from typical plants to make them subject to natural selection. (6) Accordingly, in nature all unfit mutants are likely to be eliminated by natural selection.

The mutation theory of the present day lays emphasis upon small rather than large mutations on the ground that in nature radical changes from the types of old-established species will tend to be eliminated at once by natural selection; but that minute mutations which are either neutral or advantageous in their effects may gradually accumulate, first causing new varieties to appear, then new subspecies and finally new species. At any point in the process natural selection may operate to preserve or eliminate the new forms. The problem of how evolution comes about is still an open one upon which a great number of biologists are actively at work.

Mendelian Inheritance.—A large part of the work which is being done to-day in the experimental study of evolution, as well as of the practical work of the plant and animal breeder, is based upon the remarkable discoveries of the Austrian monk, Gregor Johann Mendel. His experiments had to do with the manner of inheritance of certain characters by the individuals resulting from the crossing (hybridizing) of two organisms differing in one or more characters. His most important work was with the garden pea (*Pisum sativum*). His discoveries, the outcome of eight years of breeding experiments, were published in an obscure scientific periodical in 1866. Partly on that account and partly because the time was not yet ripe for a proper appreciation of its significance, his work remained practically buried for thirty-five years. In 1900, sixteen years after Mendel's death, his publication was discovered almost simultaneously by three botanists, who had been led by their own studies to conclusions similar to his.

A discussion of his work can best be introduced by an account of some of his experiments.

His first experiments were made by crossing two varieties of garden peas, a dwarf variety (20–45 cm. high) and a tall variety (175–200 cm. high). That is to say, he grew plants of these two varieties and used the pollen from each to pollinate the flowers of the other variety. Peas were favorable plants for his study because the pea is a species which is naturally self-pollinated. On that account, it was reasonably certain, since the seeds produced naturally by the tall variety and the dwarf variety always produce plants which are respectively tall and dwarf, that the varieties were pure as regards tallness and dwarfness.

Mendel kept a very careful record of the progeny of all his hybrids. He found that, whether he used pollen from a dwarf plant to pollinate the stigma of a tall plant or vice versa, the seeds formed gave on ger-

mination only tall plants. In different form, these results may be stated thus: When the dwarf variety was crossed with the tall variety all of the individuals of the first (hybrid) generation, commonly spoken of as the F_1 (first filial) generation, were tall (Fig. 411, second row from top of figure).

In the F_2 (second filial generation), secured by allowing F_1 individ-

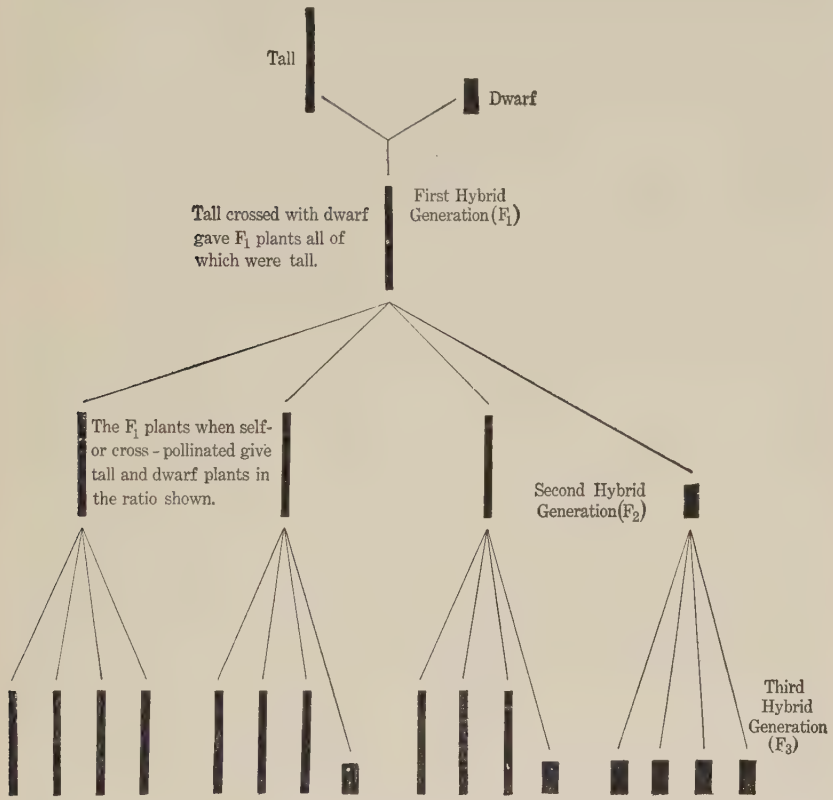


FIG. 411.—Diagram to illustrate inheritance in a monohybrid cross between tall and dwarf peas.

uals to self-pollinate, about one-quarter of the individuals were dwarf and about three-quarters tall (third row, Fig. 411). Mendel secured 787 tall to 277 dwarf plants. When the F_2 dwarf plants were self-pollinated, all their progeny were dwarf plants. These dwarf F_2 and F_3 plants were like the dwarf plants which were crossed with the tall plants at the beginning of the experiments and they never gave any tall plants as long as they were bred with dwarf plants. Two-thirds of the

tall plants of the F_2 generation (that is, one-half of all the F_2 individuals), when self-pollinated, gave one-quarter dwarf and three-quarters tall plants. The remaining tall F_2 plants, when self-pollinated, gave nothing but tall plants, which like the dwarf F_2 plants, gave nothing but tall plants when self-pollinated. In short, although the F_2 plants appeared to be only of two kinds, dwarf plants and tall plants, there were actually three kinds of plants. (Bottom row, Fig. 411.)

(1) Dwarf plants (about one-quarter of all) which gave only dwarf plants when self-pollinated.

(2) Tall plants (about one-half of all the F_2 plants) which when self-pollinated, gave one-quarter dwarf and three-quarters tall plants.

(3) Tall plants (about one-quarter of all of the F_2 plants and in appearance like the other tall plants) which gave only tall plants when self-pollinated.

For these three kinds of plants it is convenient to use the following designations, the meaning of which will shortly be made clear:

(1) **Pure recessives**, (2) **Hybrids** and (3) **Pure dominants.**

It is important to bear in mind that the pure recessives, when self-pollinated or cross-pollinated among themselves, will never give anything but pure recessives, in this case dwarf plants; that the hybrids, when self-pollinated or crossed among themselves, will give the three classes in the proportion 1 : 2 : 1; and that the pure dominants, when self-pollinated or crossed among themselves, will give only pure dominants.

Mendel secured results like those just described when he crossed pea varieties having smooth and wrinkled seed coats, and with others characterized by green and yellow cotyledons.

Such characters as those of tallness and of dwarfness in Mendel's peas, when inherited, remain distinct and are thus transmitted as integral units. From the fact that the tall F_1 plants gave some dwarfs when self-pollinated, it is clear that the character for dwarfness was transmitted through the tall F_1 plants as a unit which was not affected by its association with the character for tallness.

One of the most remarkable facts about Mendel's breeding experiments with tall and dwarf peas is that although the F_1 plants had received both the character for dwarfness and the character for tallness, the plants were actually tall; that is to say, the character for tallness prevented the opposite character form coming to expression. On this account, the character for tallness is spoken of as a **dominant character,** and that for dwarfness as a **recessive character.** This prevention of the expression of a recessive character by a dominant character does not always occur in Mendelian inheritance. For instance, when the

red-flowered variety of the common garden four o'clock is crossed with the white-flowered variety, the F_1 plants are pink, neither color being dominant.

Explanation of Mendel's Results on the Basis of Chromosome Behavior.—It will be recalled that, with a few exceptions, inherited characters are conditioned by genes which are transmitted from one generation to the next through the chromosomes. That is to say, the progeny have a certain character which was possessed by one or both

FIG. 412.—Chromosome individuality as shown in *Crepis capillaris* (left) and *C. setosa* (right). The two chromosomes connected by dotted lines to a single Roman numeral are homologous. Each of the chromosomes has already begun to split since the stage of mitosis shown is the metaphase of somatic (2x) nuclei. The chromosomes are shown as seen from a point on the axis of the spindle. Note the similarity in size and form of the two chromosomes in each homologous pair. The use of the same numerals in the left-hand and the right-hand part of the figure is not meant to indicate corresponding chromosonies. Compare text, page 573. (From Collins and Mann, in *Genetics in Relation to Agriculture* by Babcock and Clausen, McGraw-Hill Book Co.)

parents because the nuclei of the new plants contain chromosomes received from the parents. Now, there can be little doubt that there is a certain definite and fixed part, or **factor,** of one of the chromosomes, at least, which is the carrier of each of the two characters which distinguished Mendel's dwarf and tall varieties. The nuclei of the dwarf sporophyte plants, in his first cross, contained two homologous chromosomes each with the factor for dwarfness. In these nuclei, there were no factors for tallness. That is to say, these plants were **homozygous** for this character. The original tall plants were also homozygous because their nuclei contained no chromosomes containing a factor for dwarfness but two homologous chromosomes bearing the factor for tallness. Since these plants are naturally self-fertilized, there is little possi-

bility, under normal conditions, of the introduction into the nuclei of the progeny of dwarf plants of a chromosome with the factor for tallness. Accordingly, they produce only dwarf plants, i.e., "breed true." For the same reason, the original tall plants would also breed true under normal conditions.

The student will also recall that in the reduction division, a little before the formation of microspores (pollen grains) and megaspores (one of which gives rise to the embryo sac), the members of each pair of homologous chromosomes are separated from each other and pass to opposite ends of the spindle. Accordingly, the megaspores and microspores (and the same is true of the sperm nuclei and egg nucleus), each contain only one chromosome from each pair existing in the sporophyte nuclei. Since both the chromosomes of the homologous pair carrying the factors for stature in the sporophyte of the dwarf plants carry the factor for dwarfness, the egg nuclei and the sperm nuclei are all alike with respect to the factors for stature. Similarly, all the sperm nuclei and egg nuclei produced by the tall plants are alike in that they have the factor for tallness only.

It will make the rest of our explanation somewhat easier to grasp if we substitute the capital letter *T* for the expression "factor for tallness," and the small letter *d* for the expression "factor for dwarfness," the capital letter indicating that the corresponding character is dominant, and the small letter that the alternative character which it represents is recessive. It will also be convenient to designate the gametes bearing one of these factors as *T* sperm, *T* egg, *d* sperm and *d* egg, and the zygotes resulting from their fusion as *dT* zygotes, *dd* zygotes and *TT* zygotes.

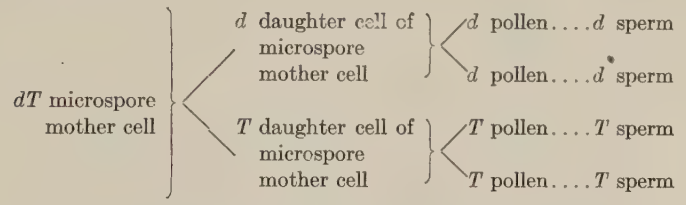
The fact already stated, that Mendel's original dwarf plants bred true, can be restated thus, using the designations just mentioned. Since, in the case of the sporophytes of the dwarf, both members of the pair of homologous chromosomes controlling stature bear the factor for dwarfness, only *d* sperms and *d* eggs will be produced by the dwarf plants produced by self-pollination or crossing with other dwarf plants. Therefore all the zygotes which are formed by the fusion of these gametes will be *dd* zygotes and will give dwarf plants.

As stated in earlier chapters, the double number of chromosomes in the zygote of any plant consists of pairs of homologous chromosomes, one chromosome of each pair having come from the sperm and one from the egg cell.

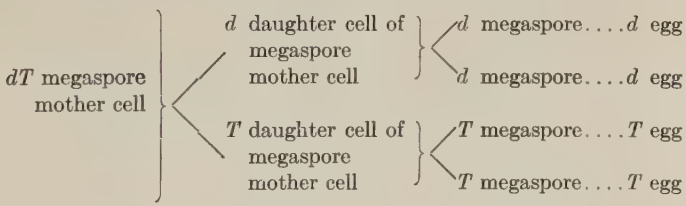
The F_1 Generation.—Now when dwarf and tall plants are crossed, pollen from the dwarf variety may be used to pollinate flowers of the tall variety, in which case *d* sperm $\times$ *T* egg = *dT* zygote; or pollen from

the tall variety may be used to pollinate flowers of the dwarf variety, in which case T sperm $\times$ d egg $= dT$ zygote.

In both cases the zygote contains a pair of homologous chromosomes, each of the members of which bears one of the alternative factors. Accordingly, the F_1 plants developed from these zygotes will be **heterozygous,** and on account of the dominance of the tall character will be tall plants. Now at the reduction division of the microspore mother cell, the d chromosome and the T chromosome, which have been associated as homologous chromosomes in all the nuclei of the sporophyte plants, are separated thus:



As a result, the pollen grains and the sperm cells are of two kinds, T and d, produced in equal numbers. Similarly there are produced T eggs and d eggs in equal numbers, as is shown in the following diagram.



Such separation, at the time of the reduction division, of the two members of a pair of homologous chromosomes bearing alternative factors, so that half of the gametes have the factor for one character and half, the factor for the other character, is spoken of as **segregation.** The resulting purity of the gametes is one of the most important features of Mendelian inheritance.

The F_2 Generation.—Now, when an F_1 plant is self-pollinated or cross-pollinated with other F_1 plants, there will be four possible combinations of sperm and egg, since there are two kinds of sperms and two kinds of eggs; and these combinations, by the law of probability, will occur in equal proportions. These combinations are:

(1) T sperm $\times$ T egg giving TT zygote.
(2) d egg $\times$ T sperm giving dT zygote.
(3) T egg $\times$ d sperm giving Td zygotes, and
(4) d sperm $\times$ d egg giving dd zygotes.

These four combinations and their origin may be shown graphically by the following checkerboard diagram. In this the two kinds of sperms are placed in the horizontal row, and the two kinds of eggs in the vertical row, the possible combinations of gametes are shown in the four squares:

	T	*d*
T	1 *TT*	3 *Td*
d	2 *dT*	4 *dd*

sperms

eggs

Let us consider briefly the result of these four combinations as they are expressed in the individuals of the F_2 generation. Combinations 2

Fig. 413.—Spreading and erect pure lines of Gypsy wheat, 1907. (From Williams in *Genetics in Relation to Agriculture* by Babcock and Clausen, McGraw-Hill Book Co.)

and 3 are identical, since in both there is a chromosome bearing the factor for dwarfness and a chromosome with the factor for tallness.

These zygotes are said to be **heterozygotes.** Together, these plants will make up half of all the plants. They will all be tall plants on account of the dominance of tallness. In fact, these plants are the ones which we designated earlier as the **hybrid,** F_2 plants. They are identical with the F_1 plants in appearance and in their behavior when interbred.

The zygotes resulting from combination 4 will develop into plants

FIG. 414.—Typical heads from seven pure lines of Defiance wheat. (From *Genetics in Relation to Agriculture* by Babcock and Clausen, McGraw-Hill Book Co.)

homozygous for this character, since in this case both the members of the pair of homologous chromosomes governing stature bear the same factor. They will be dwarf plants, since the dominant character is entirely absent, and on the same account tall plants can never arise from them as long as they are interbred. These are the plants which were designated in an earlier paragraph as **pure recessive plants.** They are indistinguishable in appearance, and in their behavior when interbred, from the original dwarf plants used at the beginning of the experiment.

The zygotes resulting from combination 1 will be homozygous also,

and will correspond in their behavior with the pure recessives, except that they and their progeny will all be tall plants instead of dwarf. They are the plants that were spoken of in an earlier paragraph as the pure dominants and are indistinguishable from the original tall plants used at the beginning of the experiment.

We have described at some length the simplest possible case of Mendelian inheritance. Reference has already been made to other cases, such as varieties of peas with green and yellow cotyledons and those with smooth and wrinkled seeds. Crosses between such plants as these, which differ in one pair of contrasting characters, are called **monohybrid crosses.**

Dihybrid.—Mendel also carried on experiments in which two pairs of contrasting characters were involved, instead of one pair only. He crossed a variety which produced yellow, wrinkled seeds when self-pollinated, with another variety producing green, smooth peas. Such a cross is known as a **dihybrid cross.** Mendel could judge of the nature of the F_1 plants of this cross without planting the seeds, for the characters involved were really characters of the embryo sporophyte within the seeds and not characters which, like stature, could only be judged after germination had taken place and the embryo sporophytes had grown to some size. All the F_1 seeds from Mendel's dihybrid cross of yellow wrinkled and green smooth were yellow smooth peas. Accordingly it is clear that the characters for green color and wrinkled surface are recessive and those for yellow color and smoothness are dominant.

Now, in every nucleus of the embryo sporophyte and later of the mature sporophyte of these F_1 plants, there must have been a chromosome carrying the factor for yellow, one carrying the factor for wrinkled surface (these two chromosomes being from one parent), a chromosome carrying the factor for green color and one carrying that for smooth surface (these two chromosomes having come from the other parent). Of these four chromosomes, the ones carrying the color factors would constitute a homologous pair, and the other two also a homologous pair. When these seeds were germinated and the resulting plants had flowered, there would be, at the reduction divisions, as in the monohybrid case, a separation of the chromosomes of the homologous pairs, and accordingly a separation of the factors which these chromosomes carried. There would result, however, not two kinds of eggs and two kinds of sperms but four kinds of each, thus: *Ys* eggs, *Yw* eggs, *gS* eggs and *gw* eggs; and *YS* sperms, *Yw* sperms, *gS* sperms and *gw* sperms.

It is possible to prophesy what would be the various combinations resulting from the self-pollination of the F_1 plants or from crossing them with each other. The checkerboard diagram below shows the

various combinations in the simplest fashion possible. In a vertical row to the left of the checkerboard are indicated the four different kinds of eggs, and in a horizontal row above the checkerboard are shown the four types of sperms. In the sixteen blocks of the checkerboard are shown the various possible combinations which might result in the zygotes.

	YS sperm	Yw sperm	gS sperm	gw sperm
YS egg	YSYS 1	YwYS 5	gSYS 9	gwYS 13
Yw egg	YSYw 2	YwYw 6	gSYw 10	gwYw 14
gS egg	YSgS 3	YwgS 7	gSgS 11	gwgS 15
gw egg	YSgw 4	Ywgw 8	gSgw 12	gwgw 16

Examination of the diagram shows the combinations which should result and the number of each (on the average) among sixteen zygotes or F_2 seeds.

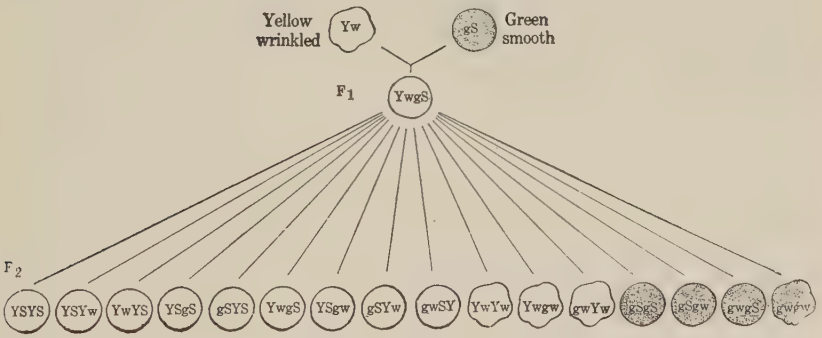


FIG. 415.—Diagram to illustrate inheritance in a dihybrid cross between a pea which would have produced yellow wrinkled seeds if self pollinated and one which would have produced green smooth seeds if self pollinated. Wrinkled seeds are distinguished from smooth by their outline and green from yellow by the shading of the former. The letters show the various combinations of factors.

Merely for convenience in pointing out the different combinations, the squares of the checkerboard are numbered from 1–16. It will be clear that the order in which the factors are given in the different combinations is of no significance. Thus *YSYw* (square 2) is identical

with *YwYS* (square 5). The following are the combinations theoretically possible:

(I) *YYSS* (square 1)—**one zygote out of sixteen**—homozygous for both color and surface—**the seed yellow and smooth.**

(II) *YYSw* (squares 2, 5)—**two zygotes out of sixteen**—homozygous for color but heterozygous for surface—**the seed yellow and smooth**—the latter on account of dominance of the smoothness.

(III) *YgSS* (squares 3, 9)—**two zygotes out of sixteen**—homozygous as to surface character but heterozygous for color—**the seeds yellow and smooth**—the former on account of the dominance of yellow color.

(IV) *YgSw* (squares 4, 7, 10, 13)—**four zygotes out of sixteen**—heterozygous as to the characters both for color and surface—**the seeds yellow and smooth**—on account of the dominance of these characters.

(V) *YYww* (square 6)—**one zygote out of sixteen**—homozygous as to both color and surface—**the seeds yellow and wrinkled** because of the absence of chromosomes bearing either the factor for green color or for smooth surface.

(VI) *Ygww* (squares 8, 14)—**two zygotes out of sixteen**—heterozygous for color and homozygous for surface—the seeds **yellow** on account of the dominance of yellow and **wrinkled** because no chromosome with the factor for smoothness is present.

(VII) *ggSw* (squares 12, 15)—**two zygotes out of sixteen**—heterozygous as to surface and homozygous as to color—**the seeds smooth** on account of the dominance of this character and **green** because of the absence of any factor for yellow.

(VIII) *ggSS* (square 11)—**one zygote out of sixteen**—homozygous both as to color and surface—**the seeds therefore green and smooth.**

(IX) *ggww* (square 16)—**one zygote out of sixteen**—homozygous both as to color and surface—seeds therefore **green and wrinkled.**

Now, although there are nine different sorts of zygotes in respect to chromosomes present in their nuclei, the seeds, as regards the characters which will be visible, fall into four classes only, as follows:

Classes according to the appearance of the seeds.	Combinations of Factors
A. Yellow smooth (9 seeds)	1. YYSS —1 seed 2. YYSw —2 seeds 3. YgSS —2 seeds 4. YgSw —4 seeds
B. Yellow wrinkled (3 seeds)	5. YYww—1 seed 6. Ygww —2 seeds
C. Green smooth (3 seeds)	7. ggSw —2 seeds 8. ggSS —1 seed
D. Green wrinkled(1 seed)	9. ggww —1 seed

All plants of classes A, B and C, which are alike in all obvious characters, although they may differ in some recessive characters, are said to have the same **phenotype.** If they are also alike in all other characters, that is, in those characters which do not come visibly to expression but can be demonstrated only by breeding experiments, they are said to have the same **genotype.** Thus the individuals of any single one of the nine sorts listed under " Combinations of Factors " have the same genotype. Altogether, there are nine genotypes represented. For example, seeds corresponding to the combinations, *YYSS* and *YgSw*, have the same phenotype, because they are all yellow and smooth. However, they differ genotypically since those corresponding to the combination *YYSS* have no factor for green color and wrinkled surface, while the other seeds, corresponding to the combination *YgSw*, have these factors but do not manifest their presence because the characters for yellow color and smooth surface are dominant.

An examination of the nine combinations listed above will show that not only *YYSS* (the pure dominant) and *ggww* (the pure recessive) will breed true, but also the combinations *ggSS* and *YYww*. In other words, all will breed true in which only two factors (one for color and one for surface) are present. All the others will give various combinations when self-fertilized. These combinations can be definitely foretold on the basis of the checkerboard diagram on page 591.

Clearly, when trihybrid crosses are made, that is, crosses of individuals differing in regard to three pairs of contrasting unit characters, a much more complex situation will result in the F_2 than in the case of dihybrids. It will, however, be possible to prophesy all the resulting combinations, just as in the case of a dihybrid cross.

This account of the results of monohybrid and dihybrid crosses illustrates the manner in which many new combinations of characters may be established by crossing plants differing in relatively few characters. Thus the crossing of forms differing in two such pairs of contrasting characters gives four possible combinations of characters. Eight combinations of factors result when the forms crossed differ in three pairs of contrasting (alternative) characters and sixteen if four pairs are involved. It is thus that new characters such as those which have originated in the sweet pea by mutation have been utilized in producing numerous varieties.

INDEX

(An asterisk (*) indicates an illustration)

A

Abies, 526
  absence of root hairs in, 169
Absciss layer, 203, *204
Absorption, 17, 61, 70
  by plant cells, a summary, 71
  by roots, 21
  of inorganic salts, 177
  of water, 169
  process of, 172
Acer, accessory buds of, 26
  fruit of, 273, *293
  leaf of, 188
  saccharum, wood of in section, *121
  samara of, 273, *293
Accessory bud, 26
Accessory pigments, 247
  function of, in red algae, 383
Acetic acid fermentation, 399
Acids, plant secretions, 219
  various. See Acetic, Malic, etc.
Acorn, *281
Actinomorphic flower, *246, *250
Actinomorphy, 564
Active buds, 28
Active solute absorption, theory of, 71
Adaptations favoring dispersal of seeds by wind, water and animals, 292
Adder's tongue fern, 490
Adiantum, 509
Adnation, 238
Adventitious buds, 26
Adventitious roots, 153
Aecidiospores, *442, 443, 444
Aecidium, *442, 443, *445
Aerial roots of banyan, *179
  of corn, *178
Aesculus, bud scales and leaves of, *182
  twigs of, showing opening of terminal bud, *92
After-ripening of seeds, 305
Agaricales, 446
Agaricus campestris, 446, 451
Age and vitality of seeds, 304
Age of trees, determining, 115
Aggregate fruits, 272, 274, *275
Agronomy, 5
Agropyron repens, rhizome of, 21, *146
Air in the soil, 309, 319
  composition of, 205
  movements, as influencing transpiration rate, 222–223
  temperature of, 320
    as factor influencing transpiration rate, 22, 223
Akene, 274, *281
Albugo candida, *413, *414
Alcoholic fermentation, 398
Alder, section of old root of, 164
Aleurone grain, *290
Alfalfa, cross section of stem, *131
Algae, 343–389
  alternation of haploid and diploid phases, 388
  blue-green, 347–351
  brown, 372–381
  characteristics of, 346
  classes of, 346
  conditions favoring zoospore and gamete production in, 388
  green, 351–371
  principal features in the evolution of, 386
  probable origin and relationship of, 389
  red, 382—385
  reduction division in, 360, 365, 381, 385
  relative complexity of, and typical land plants, 388
Algal-like fungi, 410, 422
Alkaloids, 219

Allium cepa, bulb of, 21, *149
cell from tip of root of, *43
Almond, fruit of, 278
Alnus, cross section of old roots, *164
Aloe, monocotyledon with cambium ring, 130
Alternate buds, 27
Alternation of generations, in *Bryophyta*, 458
in *Pteridophyta*, 521
in *Rhodophyceae*, 383
Alternation of haploid and diploid phases in life history of algae, 388
Aluminum, 327
Amanita, characteristics of, 453
Amino-acids, 298, 397
Ammophilla arenaria, *178
Ampelopsis, air roots of, 32
Amygdalin, 219
Amylase, 298
Anabolism, 75
Anagallis, sessile leaves of, *183
Analogous organs, 338
Anaphase, 79
Anatomy, 5
Anatropous ovule, *243
Anchorage by roots, 21, 179
Androsporangia of *Oedogonium*, *366
Angiospermae, 525, 545–570
Angiosperms and gymnosperms, distinction between, 546, 562
evolution of, 563–568
Animals, as a factor in seed and fruit dissemination, 292
Annual rings, *111, *113, *115, *116, *123
Annuals, 40
Annulus of fern sporangium, *498, *499
of moss capsule, 481, *482
Anther, *235
cross section of open, *240
longitudinal section of, in wheat, *547
stages in development of, in wheat, *546
versatile, 256
Antheridia, of *Albugo*, *414
Bryophyta, 458
Equisetum, *512
Fucus, *379
Funaria, *477, *478
Antheridia, of *Marchantia*, *468
Oedogonium, *365, *366
Polypodium, *494
Riccia, *461
Saprolegnia, *412
Selaginella, 517
Vaucheria, *389
Antheridial cell, 534
Anthoceros, *471, *472, *473, 489
Anthocyanin pigments, 54
Anthrax, 564
Antipodal nuclei, *236, 244
and synergids, fate of, 265
in corn, *555
Apical growth, 134
meristem, 102
Apetaly, 564
Apocarpy, 564
Apophysis, 480, *481
Apothecium of *Ascomycetes*, 423
of lichen, *434
Apple, development of flower and fruit, *279
fruit spur of, *29
mature fruit, *280
mixed buds of, 28
Applied science, 4
Archegonial receptacle of *Marchantia*, *469
Archegonium, of *Bryophyta*, 458
Equisetum, 512, *513
Funaria, *476, *477
Pinus, *537
Polypodium, 494, *495
Riccia, 461, *462
Selaginella, *515
Archesporial cells of wheat, *546
Arcyria, a myxomycete, 407
Artemisia vulgaris, leaf variation in, *574
stem section, *130
Aristolochia, longitudinal section of terminal bud, *89
section of vascular bundle, *99
Aristotle, 10
Artificial classification of organisms, 11, 340
Arundinaria, parallel veining in leaf of, *187
Ascent of sap, 136
Asclepias, latex in, 142

Asclepias, seed of, *293
Ascocarp, 423
Ascomycetes, 422–435
Ascospore, 423, *425, *427
Ascus, 423, *425, *427
Asexual reproduction, definition of, 344
  by spores, 344
Ash, fruit of, *293
  twigs of, showing opening of terminal bud, *91
Asparagus, cladophylls of, *232
  scale leaves of, *232
  seed, cells from endosperm of, *287
Aspergillus, 427, *429
Assimilation, 17, 76
  and seed germination, 299
Association, of plants, 329
Atmosphere, composition of, 205
Atmospheric humidity, 309, 314
Atoms and molecules, 4
Arropous ovule, *243
Auricles, of grass leaf, *189
Autoecious fungi, 444
Autophytic plants, 341
  thallophytes, 346
Auxospore of diatoms, 371
Available water in soil, 173, 309, 317
Avena sativa, inflorescence, spikelet and flower of, *247
Avocado, mixed buds of, 28
Avogadro's law, 214
Awn, of grasses, *256
Axile placentation, *242
Axillary bud, 26
Azalea, capsule of, *273
Azolla, a water fern, 507
Azotobacter, 401

B

Bacillus forms of bacteria, 393, *394
Bacteria, 392–406
  beneficial activities of, 395
  distribution of, 392
  form types of, *393, *394
  general characteristics of, 392
  germination of spores of, 395
  harmful activities of, 396
  in relation to soil fertility, 399
  motility of, 395
  multiplication of, 393
Bacteria, size of, 393
  spore formation in, 394
  structure of cell of, 393
Balance between shoot and root systems, 21
Bamboo, parallel veining in leaf of, *187
Banner of pea flower, *250
Banyan, aerial roots of, *179
  tree, air roots of, 32, 179
Barberry, leaf spines of, *227
Barley, leaf of, *189
  reproduction by means of roots in, 180
  root of, cross section, *161
  root of, longitudinal section of, *158
  smut, *440
Bark, 93, 120
Barriers, kinds of, 330
Basidiomycetes, 435–456
Basidiospore, 435, 441, *442, *450
Basidium, definition of, 435
  -forming fungi, 435–456
  stages in development of, *450
Basswood, diagram of three-year-old stem of, *124
Bast fibers, *83, *107
Beach grass, *178
Bean, seed of, *284, 288
  stages in germination of seed, *306
Beet, flower of, *248
Begonia, adventitious roots from leaves, 154
  fleshy storage stems, 141
Bentham and Hooker, 10
Benthon, 346
Berberis vulgaris, *442, 443, *445
  leaf spines, *227
  reproduction by means of roots, 180
Bermuda grass, ligule of leaf, 189
Berry, a type of fruit, 272, 276
Beta vulgaris, flower of, *248
  storage root of, 21
  tap root system of, *154
Betula, lenticels of, 128
Bidens, seeds of, *293
Biennial, 40
Bifacial leaves, 198
Bilateral symmetry, *250, 251
Binomial nomenclature, 14
Biology, 4
Biotic factors, 309, 310

Biotic factors, influence of, upon plants, 322
  successions, 331
Birch, lenticels of, 128
Bird's nest fungi, 456
Bittersweet, a liana, 24
Blackberry, fruit of, *275
  mixed bud of, 28
Black locust, "suckers" in, 180
  stipular spines of, 186, *227
  tyloses in tracheal tubes, *126
Black spore stage of *Puccinia graminis*, 441, *442
Black stem rust of wheat, 441–445
Bladderwort, insectivorous plant, 229, *232
Bladder wrack, 375
Blazing star, root system of, *156
"Bloom," 224
Blue-green algae, 347–351
Blue molds, 427
Body cell in pine, *536, 538
Border parenchyma, *200, 201
Bordered pit, diagram showing structure of, *104
Boron, 327
Botany, definition of, 2
  subdivisions of, 5
  systematic, 5
Botrychium, 490
Box elder, accessory buds of, 26
Brace roots, 32
Bracken fern, 509
Bracket fungus, *454
Bract, 234, 256
Bracteal leaves, 32
Branch bud, 27
  root development of, *165, *166, *167
Branching, types of, 24
Brassica, phototropic curvature of seedling, *35
  silique of, *273
Brassica rapa, storage root of, 21
Bread mold, *415–*419
Briggs and Shantz, wilting coefficient, data from, 174, 175
Bromine, 327
Brownian movement, 361
Brown, Robert, 58
Brown algae, 372–381
Brown rot of stone fruits, 424
Bryales, 474
Bryophyllum, adventitious roots from leaves, 154
Bryophyta, 13, 457–488
  characteristics of, 457–459
  classes of, 459
  summary of, 486–488
Buckeye, bud scales and leaves of, *182
Buckeye, twigs showing opening of terminal bud, *92
Buckwheat, akene of, *281
Budding, 144
  in yeast, 430, *431
Bud grafting, *25
  mutants, 577
  scale scars, 31
  scales, 182, 226
  terminal of *Aristolochia*, *89
  terminal of *Elodea*, *90
  variation, *578
Buds, 24, 30
  classification of, 26–30
  of peach twig, 27
Buffalo berry, epidermal hairs, 197
Bulb, 21, 148
  of onion, *149
Bundle scar, 30, 204
Bundles, closed, 129
  open, 129
Bunt of wheat, *437, *438

C

Cabbage, club root of, *408, *409
Cactus, fleshy storage stems, 141
  giant, an extreme xerophyte, *228
Caffein, an alkaloid, 219
Calamites, 509
Calcium, 325, 327
Calla lily, flower stalk of, showing tissue tissue tensions, *127
Callose, 86
Callus, 86, 143
Calorie, definition of, 221
Calyptra, of *Funaria*, 470, *474
  of *Marchantia*, 470
Calyx, *235
Cambium, 80, 95, *96, *97, *98, *99, *107, *108, *109
  cork, 106, *109, 110, *112

Cambium, differentiation of cells, *108
fascicular, 95, *96
origin of, in root, *162
vascular, 93, 106
Cambium ring, 106
Campyloptropous ovule, *243
Canada thistle, rhizome of, 21, 145
Canna, starch from rhizome of, *286
Capillarity, 137
Capillary water, 172
Capillitium, *407
Capsella, origin and development of flower parts, *237
rosette in, 41
stages in development of embryo, *266
unicellular hair of, *198
Capsule, type of fruit, *273, 274, 279
fern sporangium, *498, *499
Marchantia, 469, *470
moss, *480, *481
sphagnum, *485
Carbohydrates, chemical nature of, 45
fermentation of, 398
food stored in seeds, 285
rate of production of, 216
a reserve food, 218
Carbon compounds, 45
Carbon cycle, *403, 404
Carbon dioxide, apparatus to demonstrate evolution, in excretion of from roots, 177
an environmental factor, 309, 314
in photosynthesis, 72, 73, 205, 216
movement of, 206
a raw material, 325
respiring seeds, *299
Cardinal temperatures, 310
for seed germination, 296
Carduus arvensis, rootstock of, 21, 145
Caroline poplar, excurrent type of stem, 24
Carotin, 50, 239, 352
Carpellate, strobili of pine, 526–*529
Carpels, 241, 242
Carpogonia, or red algae, 383, *384
Carpospore, 383, *384
Caruncle, *289
Caryopsis, 274, *281
Castanea chrysophylla, epidermal hairs, 197
Castor oil plants, seed of, *288, *289
stages in germination of seed, *307
Catalpa, whorled buds of, 27
Catkin, 259
Cell, 18, 43–85
arrangement, as basis for plant classification, 339
division, *40, 77, 78
from flesh of tomato, *52
from palisade parenchyma of leaf, *43
from root of garden pea, *52
from root of onion, *43
history of our knowledge of, 56
physiology of, 60–79
plate, *78, 79
principal parts of, 43
stone, *84
structure, as basis for plant classification, 338
theory, 57
wall, *43, 47–*48
Cells, multiplication of, 77
Cellulose, 45, 47
Central body, in cells of *Cyanophyceae*, 347
Cereals, tillering in, *88
Cheiranthes, flower colors of, 239
Chemical formulae and equations, 44
Chemosynthesis, 404
Chemotaxis, 462
Chemotropism, 36
Cherry, flower of, *255
lenticels in, 128
Chinese primrose, leaf of, showing hydathode, *223
Chinquapin, epidermal hairs, 197
Chitin, 347
Chlamydospore, *436
Chlorella, 352
Chlorenchyma, 81
Chlorine, 327
Chondriosomes, 49, 50, *52
Chlorophyceae, 351–371
Chlorophyll, a; 50, 352, *186; b, 50, 352
function of, 209
solution, absorption spectrum of, *210
Chloroplasts, *43, *49, 50
Chlorosis, 327
Christmas fern, *491
Chromatin, 53

Chromatin, granules, *49
Chromatophore, 50
Chromoplast, 49, 50, *52
Chromosome, theory of inheritance, 573
in cell division, 77, *78, 487–491
reduction in Fucus, 381
Chromosomes, homologous, 573
Chytridiales, 410
Cilia, 344, 395
Cinchona tree, quinine, from, 219
Cinnamon fern, 507
Citric acid, 219
Cladophylls, of asparagus, *232
Cladodes, 152
Cladonia, 432
Class, 14
Classification of plants, 10–12, 338–342
artificial, 11, 340
natural, 11, 340
Clematis, cross section of stem, *129
fruit of, *293
longitudinal section of stem, *134
Climatic factors, 309
Closed smut of oats, *439
Closterium, *361, *362
Clostridium pasteurianum, 401
Closed bundles, 129
Club-root of cabbage, *408, *409
Cluster cup, 442, 443, *445
Club mosses, 514–521
Coalescence of flower parts, 238
Coccus forms of bacteria, *393
Cockle-bur, fruit of, *293
Coconut, fruit of, *271
Cocos nucifera, fruit of, *271
Coenocyte, 367
Coenogamate, 418, *419
Coleoptile, *87, 291, *302, 559
Coleorhiza, *87, 291, *302, *559
Collencyma, *82, 93, *97, 99, *205
Colletia cruciate, spines of, 150, *151
Colloidal solutions, 46
Columella, in *Anthoceros*, *471, *473
in *Funaria*, 480, *481
in *Rhizopus*, *416, *417, *418
in *Sphagnum*, *485
Comatricha nigra, *407
Combinations, 575, 576
Community, plant, 329
Companion cells, *85, 86, *99, 101, 108
origin of, *92
Complementary tissue, *128
Components, of solutions, 46, 62
Composite flower, structure of, *256, 257
Compounds, 8
Concentration of solutions, footnote 64, 65
Conceptacle, 378, *379, *380
Conducting tissues, 85
Conduction, a function of stems, 135
by roots, 178
of food, 139
Conidiophore, *413, *414 *429
Conidiospore, *413, *414, *429
Conjugation, definition of, 344
in *Closterium*, *362
in *Rizopus*, 417, *419
in *Spirogyra*, 344, *345
in *Ulothrix*, 354, *355
lateral, in *Spirogyra*, *359
Connective, of anther, *236, *240
Constancy of species, theory of, 11
Continuous or fluctuating variations, 580
Convolvulus, rhizome of, 145
Copra, 282
Coprinus, 455
sterquilinus, stages in development of basidium and basidiospores, *450
Cork, *81, 83, *96, 111, *128
cambium, 90, 92, *96, 106, 110, *112
in root, 164
development of, 111
illustrations of, from Hooke's "Micrographia," *57
oak, 83
in roots, 164
in stems, *111
Corm, *149
Corn, embryo sac of, *550, *555, *556, *557
grain of, *281
pollen tube of, *554, *556
prop roots of, 32, 154, *178
smut of, *436, 437
stem of, *132
vascular bundle from stem of, *132
Corolla, *235
Cortex, *96, *97, *98, *109
in *Fucus* plant, 378, *379

Cortex, of root, 160, *161
secondary, *109. See also Phelloderm
of stems, primary, *96, 97
Corti, 58
Cordyline, monocotyledon with cambium ring, 130
Corymb, *258, 259
Cotton, flower of, *253
Cottonwood, external view of stem, *26
leaf bud in cross section, *26
seed of, *293
winter twig of, *30
Cotyledon, 283, 284, *306, *307
of wheat embryo, *558, *559
Cotyledon orbiculata, water storage leaves of, *228
Cover cells, *462
Crepis species, chromosome individuality in, *584
Crocus, corm of, *149
Cronartium ribicola, *447, *448
Cross-pollination, 261, 564
Crystalloid, *267
Crystal sand, 55
Crystals, 54, *55
Cucumber, fruit of, *277
Cucumis sativus, fruit of, *277
Cucurbita, tendrils of, 36
maxima, epidermal hairs of, 197
sieve tube and companion cells from stem of, *85
pepo, imperfect flowers of, *248, *249
stoma of, *196
Culm, *133
Cuscuta, a liana, 24, 524, *525
Cuticle, 80, *81, *97, *195
Cuticular transpiration, 224
Cutin, 192, 224
Cutinized layer, 192
Cyanophyceae, 347–351
Cycad characteristics, 543
Cycadales, 542
Cycas, 542
Cyclamen, corm of, 21
Cylindrospermum, *350
Cyme, *258, 259
Cynodon dactylon, ligule of leaf, 189
Cyperus rotundus, rhizome of, 145
Cytase, 298
Cytology, 5
Cytoplasm, 49
general, *49
Cytoplasmic membrane, *49, 50
Czapek, 37

D

Dahlia, fleshy clustered root of, *150
Damping off, 410
Dandelion, fruit of, *293
latex tubes of, 142, *143
rosette in, 41
Darlingtonia, 229, *231
Darwin, Charles, 336
theory of natural selection, 579
Date, seed of, showing plasmodesma, *48
De Candolle, A. P., 10
Decay, 397
Definitions, their use and abuse, 6
Dehiscence, methods of, 252
of sporangium of *Polypodium*, 505
Dehiscent fruits, 273, 278
de Juissieu, Antoine Laurent, 10
Bernard, 10
Delayed germination, 304
Deliquescent type of branching, *23
Delphinium, follicle of, *273
Denitrification, 404
Density, 7
Desmids, 352, *361
De Vries, mutation theory of evolution, 581
Diastase, 297, 298, 398
Diatomaceous earth, 371
Diatoms, *370, *371
Dichotomy, in *Fucus*, 377
in powdery mildews, *427
Diclinous flower, 246
Dicotyledons and monocotyledons, distinctions between, 568
Dictyostele, *96, 105, *106
Diffenbachia, starch grains of, *286
Diffusion, 62, 63
diagram illustrating through semi-permeable membrane, *64, *67
in relation to absorption by plant cell, 67
of solutes through membranes, 66
Digestion and seed germination, 297
Digestive enzymes, 298
Digitalis, cross section of stem, *130

Dihybrids, 589
Dimorphism, leaf; *199
Dioecism, *249, 261
in *Marchantia*, 467
in *Oedogonium*, 364
in *Riccia*, 460
Dionoea muscipula, leaf of, 229, *230
Dioon, 542
Dioscorides, 10
Diospyros, mixed bud of, 28
Diplococcus, *393
Diploid number of chromosomes, 385
Direct response to environment, theory of, 577
Disc flowers, *256
Discomycetes, 423
Diseases due to bacteria, 396
Division of cells, 77
reduction, 502
Dock, cell from leaf stalk of, showing crystals, *55
Dodder, a liana, 24, 524, *525
Dominant characters, 583
Dormancy of seeds, 304
Dormant buds, 28
Dorsiventral leaves, 198
Double fertilization, 265
Douglas fir, 526
Downy mildews, 410, 419–421
Drosera, leaf of, 229, *231
Drupe, 273, 277, *278
Dry fruits, 273, 278, 281
Duckweed, water roots of, 32
Dujardin, 58
Dutchman's pipe, longitudinal section of terminal bud of, *89
Dwarf males, in *Oedogonium*, 365, *366

E

Earth-star, 456
Ecballium elaterium (squirting cucumber), fruit of, *294
Echinocystis, fruit of, *273
fleshy storage stems of, *152
tendrils of, 36
Ecology, 5, 309
Edaphic factors, 309
Eel grass, marine, 525
Egg cell, definition of, 345
nucleus, *236, 244
Elaters, *470, *473, *511
Elder, lenticel in, *128
Eleagnus, hairs of, 197, *198
Elements and compounds, 8
essential and chemical symbols, 44
Elements, role of, in the plant, 326–327
Elm, bark of, 126
deliquescent type of branching in, *23
fruit of, *293
Elodea, 525
liberation of oxygen from, *214
terminal bud of, *90
a water plant, 144
Embryo, 265, 283, 284
of bean, 289
of *Capsella*, *266
of castor oil plant, *289
of corn, *281
formation of, 265, *266
organs of, *284
of pine, 539–540
of *Riccia*, *463
rudimentary, 304
of *Selaginella*, *517, 518
of shepherd's purse (*Capsella*), *266
stages in development of, *266
of wheat, 552, *558, *559
Embryo sac, 244, 245
of corn, *550, *555, *556, *557
Endemism, 331
Endocarp, *271
Endodermis, *96, *97, *98, 105, *109, *165
Endosperm, 283, 284, *287
formation of, 265
in date seed showing plasmodesma, *48
in pine, *537, *544
in seed of castor oil plant, 288
in wheat, *284, *290, 556
Energy, changes brought about by plant, 6, 7, 327–329
transformation of, 9, 323
Enertherna papillatum, *407
Engelmann's experiment, 208, *213
Engler and Prantl, 10, 341
English walnut, stone cells from, *84
Entomophthorales, 411
Environment, factors of, 309
heredity and, 39
relation of plants, to, 309–331

Enzymes, 219, 297, 298
Epiblast, *87, 291, *559
Epidermal hairs, 197, *198
Epidermis, *81, 95, *96, 160, *161, 190
Epigyny, 253, *254, 564
Epiphytes, algal, 352
Epipetaly, 253
Equations, chemical, 44
Equisetineae, 490, 509–514
Equisetum, 509–514
  arvense, *510
  giganteum, 509
  scirpoides, 509
Eribotrya japonica, fruit buds of, 27
Erysiphe, 427
Eschscholtz, 15
Essential oils, 141, 219
Eubasidiomycetes, 435, 445–456
Eucalyptus, leaf dimorphism in, *199
Euglena, *389
Euphorbia, a latex plant, 142
  leaves of, 233
  stipular spines of, 186
  storage in stems of, 141
European linden, leaf mosaic of, *184
Eusporangiate ferns, 490, 507
Evening primrose, rosette in, 41
Evolution, of the flower, 563
  and heredity, 571–593
  and natural classification, 11
  and plant relationships, 336–338
  theory of, 3
Excurrent type of branching, *22, *74
Exine, 262, *263, 464
Exoascus deformans, *423, *425
Exocarp, *271

F

Factor, 484
Faculative parasite and saprophyte, 391
Fagopyrum esculentum, akene of, *281
False indusium, 508
  mallow, epidermal hair of, *198
Family, 14
Fascicle of pine leaves, 526
Fascicular cambium, 95, *96, *97
Fatty acids, 298
Fats, 287
  chemical nature of, 45
  fermentation of, 397
  foods stored in seeds, 285, 287
Felled trees, determining age of, 115
Female gamete, defined, 345
Female gametophyte, of corn, development of, *550
  Equisetum, *513
  Pinus, 537
  Selaginella, *515, 517
  wheat, 552
Fermentation, 397–399, 430
Ferns, 490–509
Ferns and fern allies, 489–521
Fertilization, definition of, 264, 345
  in *Albugo*, 414
  double, 265, 554
  effect of, on fruit formation, 266
  Equisetum, 512
  Fucus, *377, 381
  Funaria, 479
  Marchantia, 469
  Oedogonium, 364
  Peziza, 425
  Pinus, 528
  Polypodium, 495
  Riccia, 461
  Saprolegnia, 412
  Selaginella, 518
  Triticum, 553
  Vaucheria, *369
Fibers, *83
Fibrous root system, 154, *155
Ficus, air roots of, *179
Ficus elastica, a rubber producing plant, 142
  indica, aerial roots of, *179
Fig, aerial roots of, 32
  mixed bud of, 28
  stipules of, 186
Filament of anther, *235
Filicineae, 490–509
Film water, 172
Fimbriaria, 469
Firs, 526
  absence of root hairs in, 169
Fission, definition of, 344
  fungi, 392
  in Cyanophyceae, 348
Fixation of nitrogen, 400–402
Flagellates, *389, 390
Flagellum of bacteria, 395
  of *Euglena*, *389

Fleshy and woody fungi, 445–456
fruits, 272, 276
Floral diagram, *246
leaves, 32
Florida moss, 525
Flower, 234–267
accessory parts of, 235
actinomorphic, 250
apetalous, 246
bud, *27, *28
bud scar, *30
complete, 245
composite, *256, 257
cyclic, 249
diagram of, *235, *236
diclinous, 246
definition of, 234
disc, *256, 257
essential parts of, 235
formulae, 565, *566, 567, *569
grass, *247, 255
hermaphroditic, 246
heterocyclic, 250
histology of parts, 238
imperfect, 246, *248, *249
incomplete, 245
infection in smuts, 437
irregular, 250
isocylic, 249
lacking one of the essential parts, 246
origin of, *237
parts of, *235
union of, 251
perfect, 248
pistillate, 246, *248
primordia of, *237
ray, *256, 257
regular, 250
reproduction by, 260
staminate, 246, *248
summary of process of reproduction by, 267
superior, 253, *254
symmetry of, 250
tendencies in evolution of, 563
types of, 245
Fluctuating or continuous variations, 559
Foliage leaves, 32
Follicle, *273, 279
Fomes ignarius, *454
Food, conduction of, 139
definition of, 76
kinds of stored in seeds, 285
manufacture of, by leaves, 21, 205–218
manufacture of, by stems, 135
storage, by leaves, 227
by stems, 135
transfer of, and seed germination, 298
the term, how used in this book, 76
Foot, of *Marchantia*, 469, *470
of moss, *480
of fern, 496
of *Selaginella*, *518
of *Sphagnum*, *485
Forestry, 5
Formulae, chemical, 44
floral, 565, *566, 567, *569
Fragaria, flower of, *251
fruit of, 274, *276
runner of, 21, *128
Fraxinus, fruit of, *293
twigs of, showing opening of terminal bud, *91
Free central placentation, *242
Freezing, injury from, 310
Frond, of fern, *491
of *Fucus*, *378
Fruit, aggregate, 274, *275
and seed, 268
bud, 27
classification of, 272
definition of, 268
development of, 268–272
explosive, *294
formation, effect of fertilization on, 266
multiple, 275
parthencarpic, *270
spur of apple, *29
Fucoxanthin, 372
Fucus, 375–381
development of eggs, 380
development of sperms, 379
germination of oospore, 376, *377
life history of, 376
stipe of, 377
structure of mature plant, 378
Funaria, 474–484
gametangia, *476, *477, *478
gametophyte and attached sporophyte, *474, *480

Funaria, germination of spines, 474
life cycle, 482, *483
sporophyte of, *474, *479, *480
Fungi, 391–456
Funiculus, *236, *243, *245, 284

G

Galactose, 298
Gametangium, 418
of fern, 494
of *Funaria*, *476, *477, 478
of *Marchantia*, 468
of *Oedogonium*, 363, *365, *366
of *Rhizopus*, 418
of *Riccia*, *460, *461
Gamete, definition of, 344
in *Ulothrix*, 354, *355
Gametophyte, of *Bryophyta*, 458
of *Equisetum*, 511, *512, *513
of *Funaria*, *474, *476, *477
of *Marchantia*, *467
of *Pinus*, 535–538
of *Polypodium*, *492, *493, 494
of *Riccia*, *459, *460, *461
of *Selaginella*, *515, *516, 517
of wheat, 550, 551, 552
Garden cress, germinating seeds of, *168
seedlings of, *170
Garden pea, compound leaf of, 185
chondriosomes of, *52
Gasteromycetes, 445, 455–456
Geaster, 456
Gel, 47
Gemmae, *467, 468
cups, *467, *468
General infection in smuts, 437
Generative cell in pine, *536
nucleus, *263
Genotype, 592
Genus, 13
Geotropism, 32–34
Geranium, hairs of, 197, *198
Germ tube, definition of, 345
Germination, of pollen grain, *263
delayed, 304
processes of, 297
of seed, 295
Gill, fungi, kinds of, 451
stages in development of, *449
Gill fungus, 446
Gills, 480
Ginkgo biloba, 542, 544
Ginkgoales, 542
Girdling, of stems, effect on food conduction, 139
Glasswort, fleshy storage stems, 141
Gleditsia, spines of, 150
Globoid, *288
Gloeocapsa, *349
Gloxinia, adventitious roots from leaves, 154
Glumes, *247, 255, *256
Gnetales, 542, 547
Gooseberry, fruit buds of, 27
Gossypium hirsutum, bud, *25
flower of, *253
stem, *144
Grain (caryopsis), a kind of fruit, 274, *281
Grape, a liana, 24
mixed bud of, 28
Grass flower, structure of, *247, 255
seed, *290
Gravitational water, 173
Green algae, 351–371
Green molds, 427
Grew, Nehemiah, 57
Ground meristem, 95, *96, 160
Ground cherry, fruit of, *283
Growing point of root, 157, *158
of stem, *87, *89, *90, *134
Growth, 76
apical, 134
intercalary, 134
medium of stems, 144
and seed germination, 302
Guard cells, 190, *191, *192, *193, 194, *195
Guttation, 222
Gymnospermae, 525, 526–545
and angiosperms, distinctions between, 546, 562

H

Hairs, epidermal, *198
Hakea suaveolens, stoma of, *195
Halophytes, 319
Haploid number of chromosomes, 385
"Hard seeds," 304

"Hardening" of transplants, 311
Haustoria, of *Albugo candida*, *413
of *Peronspora*, *426
Head, *256, 257, *258, *259
Heartwood, *94, 109, *113, 119
Heat, an environmental factor, 309, 310
Helianthus tuberosus, flower of, *256
Hemibasidiomycetes, 435, 436–439
Hemicelluloses, 285, 286, *287
Hemizonia, secretion from glandular hairs, 198
Hepaticae, 459–473
Herb, 24
Herbaceous dicotyledonous stem, structure of, 128
Heredity and environment, 39
and variation, 571
Hesperidium, 272, 277
Heteroecism, 444
Heterocyclic flower, *250
Heterocyst, *350
Heterogamete, definition of, 345
in *Oedogonium*, 363
Heterophytic thallophytes, 346
plants, 341
Heterosporus ferns, 493, 507
Heterostyly, *262
Heterothallic molds, 419, *420
Heterozygous, 586
Hevea brasiliensis, a rubber producing plant, 142
Hilum, *284, 288, *289
Histology, 5
Holdfast, 354, *355, *364
Homothallic molds, 419
Hordeum sativum, root of, *158
Hormogonium, 350
Homologous chromosomes, 573
organs, 338
Homosporous ferns, 493, 507
Homozygous, 584
Honey locust, spines of, 150
Hooke, Robert, 56
Hop, a liana, 24
Hordeum, leaf of, *189
Horse mushroom, spore dispersal, *452
Horsetails, 509–514
Horticulture, 5
Host, 391, 409, 419, 425, 436, 438, 440
Huckleberry, flower of, *252
Humidity of atmosphere, as affecting rate of transpiration, 222, 315
relative, 315
Humulus, a liana, 24
Hybrids, 583
Hydathode, 222, *223
Hydnum, 455
Hydration, 47
Hydrolysis, 141
Hydrophytes, 319
Hydrotropism, 35
Hygroscopic water, 172
Hymenium, 424, *444, *451
Hymenomycetes, 445, 446–455
Hyphae, 410, 411, *413, 418, 421, 423, 425, *429, *434, *436, 456
Hypocotyl, 283, 285, *306, *307
Hypoderm, 249
Hypogyny, 253
Hypothesis, 1

I

Illumination, factor affecting photosynthesis, 216
Imperfect flower, 246
Inclusions, 43, 49, 53–56
Incomplete flower, 245
Indehiscent fruits, 274, 281
Indian banyan, *179
Indusium, of fern sorus, *498, 508
Inheritance, chromosome theory of, 573
Mendelian, 582
Inhibition, 68
Indian Pipe, 524
Infection, modes of, in smuts, 437
Inferior ovary, *234
Inflorescences, 235, 257, *258, 259
Inky cap, 455
Inorganic salts, absorption of, 177
Insect pollination, 261
Insectivorous plants, 229, *230, *231, *232
Integuments, 244, *245, *555
Intercalary growth, 134, 181
meristems, 134
Interfascicular cambium, *96, 106, *107
Internode, 19
Intine, 272, *263, *464
Invasion, plant, 330
Iodine, 327
Ipomoea batatas, storage root of, 21, 180

Iris, rhizome of, 21, *145
Iron, 325, 327
Irregular flower, *250
Irritability, 36
Isobilateral leaves, 199
Isocyclic flower, 249
Isogamete, definition of, 344
Isthmus, in desmids, *361, 362
Iva axillaris, rhizome, of, 145

J

Jacket cells in pine, 537
Janseen brothers, 56
Jerusalem artichoke, flowers of, *256
Johnson grass, rhizome of, 145
Juglans, fruit buds of, 27
  leaf of, *188
Juglans cinerea, abscission layer, *204
Juglans regia, stone cells from, *84
Juniper, 526
Juniperus, 526
Jussieu, de, Bernard and Antoine, 10

K

Katabolism, 75
Keel, of pea flower, *250
Kelps, 372, *374, *375
Key fruit, *273, 274
Key to principal types of racemose inflorescences, 259
Koch, pioneer bacteriologist, 395

L

Lactic acid fermentation, 399
Lamarck, theory of, 336, 578
Lamina, 183
Laminaria, a kelp, 372
Larch, 526
Larix, 526
Larkspur, follicle of, *273
Lateral conjugation in *Spirogyra*, *359
  meristem, 102
Latex, 141, 142, 219
Latex tubes, in root of dandelion, *143
Lathyrus odoratus, flower of, *250
  stipules of, 186, 229
  tendrils of, 229
Leaf, 181–233
  anatomy, 189, 204
  base, 183, 185
Leaf, bifacial, 198
  blade, 183, 184
    form of, 186, *188
  bud, *26, 27
  compound, 187
  defined, 181
  dimorphism, *199
  epidermis of, in surface views, 190, *192, *193
  efficiency of in utilizing sun's energy, 212
  external morphology of foliage, 183
  fall, 203
  foliage, diagram of cross section of typical, *190
  food storage of, 227
  growth of, *183
  lamina, 183
  lobed, 186
  margin, 189
  mosaic, *184, 185
  origin of, 181–183
  petiole, 183, 203
  physiology of, 205–233
  of potato in cross section, *191
  primary functions of, 205
  primordium, 181
  respiration in, 226
  scar, *30, 203
  sessile, *183
  simple, 186, *188
  special functions performed by, 226
  spine, *227
  stipules, 186
  storage of water in, 227
  tendrils, 229
  tissues in, 189
  trace, *134, *204
  types of veining in, 186, *187
  variation, *574
  vein systems, 186, *187, *202
  of insectivorous plants, *230, *231, *232
Leaf curl of peach, *412, *416
Leaflet, 187
Leaves, classification of, 32, 176
  capture of insects by, 229, *230, *231, *232
Legume, *273, 278
  flower of, *250

Lemna, *247, 256
water roots of, 32
Lenticels, *30, 31, 127
seedling of, *170
structure of, *128
Lepidium, germinating seeds of, *168
Lepidodendron, 514
Lepiota, opening of pileus, *452
Leptosporangiate ferns, 490, 499, 507
Lettuce drop, 424
Leucoplast, 49, 50, *51, *52
Lianas, 24
Liatris, root system of, *156
Lichens, 432–435
Life cycle, 40
Lifting power of transpiring leaf surface, method of demonstrating, *137
Light, 308, 311, 312
intensity, 222
Lignification, 102
Lignin, 83, 102
Ligule of grass leaf, *189
Lilac, powdery mildew, *427
Lilium, fertilization in, *556
microspore, *549
stages in development of ovule, *244
Lily, stages in development of ovule of, *244
Linnean species, 15
Linin, 49, 53
Linnaeus, *14, 15
Lipase, 298
Lip cells of *Polypodium* sporangium, *499
Liquidambar, cross section of stem, *129
Liriodendron, stipules of, 186
Liverworts, 457–473
Locule, 242
Loculicidal dehiscence, *273, 274
Lodging of grain, *39
Lodicule, *247, 256
Longevity of seed, 304
Lonicera, cross section of stem, *129
Loose smut of oats, *439
of barley, *440
Loquat, fruit buds of, 27
Lumen, *48
Lycoperdales, 455
Lycoperdon, *455
Lycopersicum, cell from flesh of fruit showing chromoplasts, *52
Lycopodineae, 490, 514–521
Lycopodium, 514, 520

M

Macrocystis, 372
Madia, secretion from glandular hairs, 198
Magnesium, 325, 327
Maiden-hair fern, 509, 542, 544
Maiden-hair tree, 544
Malic acid, 219
Malpighi, Marcello, pioneer plant anatomist, 57
Maltose, 298
Malvastrum, epidermal hairs of, *198
Manganese, 327
Man-of-the-earth, 180
Mannose, 298
Maple, accessory buds of, 26
fruit of, *293
leaf of, *188
samara of, *273
wood of, in section, *221
Marattiaceae, 490
Marchantia, 467–473
antheridia and archegonia, *468, *469
comparison with *Riccia*, 471
gametophytes of, *467
gemmae, *467, 468
germination of spores and development of gametophyte, 471
sporophyte of, 467, *470
thallus of, *466
Marine eel-grass, 525
Marsilea, 506
Materials of plants, absorbed by green plants, 324
definition of, 7
and objects, 7
transformations of, 323
Matter, 6, 7
state of, 7
Maturity of seeds, 303
Maximum temperature, 296
Mechanical tissue, 83
Medicago sativa, cross section of stem, *131
Medulla, in *Fucus*, 378, *379
Medullary rays, *98, *107, 110, *117
Megasporangium, of pine, *530

Megasporangium, of *Selaginella*, 515
of wheat, 535
Megaspore, of corn, 536
of *Pteridophyta*, 507
of *Selaginella*, 515
of wheat, *548, *551
Megasporangiate strobili of pine, *528, *529
Megasporophylls of pine, 528, *529, *530, *533
Melilotus, tap root system of, *155
Membranes, cytoplasmic, *49, 50
nuclear, *49, 53
permeable and semi-permeable, 63, 64
Mendel, Gregor Johann, work of, 582
Mendel's results, explained on basis of chromosome behavior, 584
Mendelian inheritance, 582
Merismopedia, 349, *350
Meristems, 95
apical, 102
intercalary, 134
lateral, 102
primary, 104, 105
secondary, 110
Meristematic tissue, 80
Mesembryanthemum, water storage leaves of, *228
Mesocarp, *271
Mesophyll, 198, 200
Mesophytes, 319
Metaphase, 79
Micrographia, facsimile reproduction from, *58
Micropyle, *236, *244, *245, *284, 288, *289
Microsphaera, *427
Microsporangium, of pine, *532, 535
Selaginella, 515
wheat, 549
Microspores, of *Pteridophyta*, 507
pine, 532, *536
Selaginella, 515, 518
wheat, *549
See also Pollen
Microspore mother cells, *516, *535, *546, *547
Microsporangiate strobili, of pine, *531, *532
Selaginella, 515
Middle lamella, 47, *48
Milkweed, latex in, 142
seed of, *293
Minimum temperature, 296
Mistletoe, *524
Mitochondria, *52
Mixed bud, 27
Mixtures, 9, 45, 46
Modifications, 575
Molds, blue and green, 427–430
Molecules, 9
Monocotyledons, 568
and dicotyledons, distinctions, 568
structure of stem of, 128, *132, *133
Monoecism, 248
Monohybrid, *585, 589
Monotropa, saprophytic flowering plant, 524
Monterey pine, megasporangiate strobili of, *528
Moonwort, 490
Morning glory, rhizome of, 145
Morphine, an alkaloid, 219
Morphology, 5
Morus, fruit of, *273
mixed bud of, 28
Mosaic, *184, 185
Mosses, 473–486
Mucilage, 141
Mucorales, 410
Muehlenbeckia platyphylla, stems of, 152
Mulberry, fruit of, *273
mixed bud of, 28
Mullein, epidermal hairs of, 197
Multiple fruits, 272, *273, 275
Multiplication of cells, 77
Musci, 473–486
Mustard, geotropic and phototropic curvature of seedling, *33, *34
silique of, *273
Mutants, bud, 577
Mutation, 575, 576
theory of evolution, 581
Myxomycetes, 406–410

N

Naked bud, 25
Nasturtium, petiole as tendril, 229
Natural classification, 11, 340
Natural laws, 1

Natural selection, Darwin's theory of, 579
Navicula, *371
Neck, of archegonium, 461, *462
Neck canal cells, 461, *462, *538
Nectaries, *236, 239
Nemalion, a red alga, 424
Nepenthes, 229, *231
Nephrodium, a fern, *504
Nereocystis, a kelp, 372, *374
Net veining, 186, *187
Nicotiana, secretion from glandular hairs, 198
Nidulariaceae, 456
Nipa fruticans, stomata from leaf of, *195–225
Nitrification, 402–404
Nitrobacter, 402
Nitrogen, 325, 326
  cycle, 404, *405
  fixation, 400–402
Nitrosomonas, 402
Node, 19
Nomenclature, binomial, 14
Nostoc, 349, *350
Nucellus, *243, *245, 283, *290, *554 *555
  of pine, *537
Nuclear membrane, *49, 53
  net, *49, 53
  sap, *49, 53
Nucleolus, discovery of, 58
  structure of, 52–53
Nucleus, 49
Nut, 274, 281, 282
  grass, rhizome of, 145
Nymphaea, a water lily, *321

O

Oak, bark of, 83
  fruit of, *281
  leaf of, *188
  mixed buds of, 28
  sections of wood of, *122
Oat smut, *439
Oats, inflorescence, spikelet and flower, of, *247
Obilgate parasite and saprophyte, 391
Odors, of flowers, 239
Oedogonium, 352, 363–367
  formation and escape of zoospore, *363
  gametangia in, 363
  germination of the oospore of, 365, *366
  production of dwarf males in, 365, *366
  sexual reproduction in, 364
  significant facts relating to structure and life history of, 366
Oenothera, rosette in, 41
Oil, per cent of, in some common seeds, 288
  reserve foods, 218
  vacuole, 54
Onion, bud of, 21, *149
  cell from tip of root, *43
  stages in germination of seed, 288
Onoclea, 495, 507
  spermatozoid of, *495
Oogonium, 458
  of *Fucus*, *380
  of *Saprolegnia*, *412
Oomycetes, 410
Oosphere, definition of, 345
Oospore, definition of, 345
Operculum, *481, 485
Ophioglossum, 490
Opposite buds, 27
Optimum temperature, 296
Opuntia, stems of, *152
Order, 8
Organic evolution, theory of, 336
  principal features of, 337
Organs, analogous and homologous, 338
Organs and tissues, 17
  of typical seed plant, *20
Origin, and evolution of sex, 386–388
  of species, theories of, 577
Orthogenesis, theory of origin of species, 579
Oscillatoria, *351
Osmosis, 65
Osmotic pressure, 65
Osmunda, 507
Ostiole, 378
Ovary, *235, *236, *240, *241
Ovule, 242
  longitudinal section of, *245
  stages in development of, *243, *244
Oxalic acid, toxic to protoplasm, 55

Oxalis, leaf of, *188
Oxygen, and seed germination, 296
by-product of photosynthesis, 213, *214

P

Palea, *247, 256
Palet, *247, 256
Palisade parenchyma, *190, *191, *193, 200, 201
Palmate venation, 186
Palmitin, a fat, 45
Pandorina, 386
Panicle, *247, 255, *258, 259
Papaver, capsule of, *273
Pappus, *256, 257
Paraphyses, *477, *478
in *Fucus*, 378, *379, *380
Parallel veining, 186, *187
Parasite, definition of, 391
Parenchyma, *80
palisade, *190, *191, *193, 200, 201
spongy, *190, *191
Parietal placentation, *242
Parmelia perlata, a lichen, *434
Parsnip, storage root of, 21
Parthenocarpy, 266, 269, *270, 277
Parthenogenesis, in *Ulothrix*, 356
Pastinaca sativa (parsnip), storage root of, 21
Pea, fruit of, a legume or pod, *273
Peach twig, buds of, *27
Pear, adventitious roots from stem cuttings, 154
mixed buds of, 28
simple leaf of, *188
stem of, in cross section, *140
Pediastrum, 386
Pedicel, definition of, *235
Peduncle, definition of, 235
Pelargonium, glandular hairs of, *198
Pelagophycus, a kelp, *375
Pellionia, starch-storing cell of, *51
Penicellium, 427, *429, 430
Camemberti, 430
Roqueforti, 430
Pepo, the pumpkin, 272, *277
Peptids, 397
Peptones, 397
Perception, 36
Perennial, 41
Perfect flower, 248
Perianth, 235, 246
Pericarp, *87, 271, *290
Pericycle, 95, *96, *97, *98, *99, 100, *165
Periderm, *204
Peridium, 407, 455
Perigyny, 253, *254, *255
Perianium, of spore wall of *Equisetum*, 511
Perisperm, 283
Peristome, *481, *482
Perithecium, 423, *427, *428
Permanent wilting, 173
Peronospora schleideniana, 421
haustoria of, *426
Peronosporaceae, 419
Peronosporales, 410
Persea, mixed bud of, 28
Persimmon, mixed bud of, 28
Petals, *235, 239
color of, 239
Petiole, 185
anatomy of, *203
Peziza, 423–424
aurantiaca, 424
Phaeophyceae, 372–381
Phaius, starch grains of, *286
Phallaceae, 456
Phaseolus, example of liana, 24
lunatus, starch grains of, *286
vulgaris, seed of, *284
stages in the germination of, *306
Phelloderm, 110, 111
Phellogen, 106, 110, 112, *128
in root, 164
Phenotype, 592
Phleum pratense, ligule of leaf, 189
Phloem, 95, *96, *98, *99, 101, 105, 109
parenchyma, 101
ray, 110
tissue elements of, 101
Phoradendron, *524
Phosphorus, 325, 326
Photosynthesis, 72, 205
and respiration contrasted, 75
by-products of, 213
conditions influencing rate of, 216
course of, 216
end-products of, 215
energy factor in, 207, 209
function of chlorophyll in, 209

Photosynthesis, necessity for light in, 207
rate of carbohydrate production in, 216
raw materials in, 205
utilization of the product of, 218
Phototropism, 34
Phycocyanin, 347
Phycoerythrin, 382
Phycomycetes, 410–422
summary, 421–422
Phyllactinia, 427
Phylloxera, 323
Physalis, fruit of, *293
Physiology of the cell, 60
plant, 5
Phytelephas, 282
Phytobenthon, 346
Phytophthora infestans, 420
Phytoplankton, 346
Picea, 526
Pigments, 219
accessory, 347
anthocyanin, 54
Pileus, 450
Pilularia, 507
Pimpernel, sessile leaves of, *183
Pine wood, diagram showing structure of, *116, *117
Pines, excurrent type of branching in, *22
seed of, *293, 544
Pinna, of fern leaf, 491, 498
Pinnate venation, 186
Pinus, megaspores of, *534
development of female and male gametophytes of, 535, *536
fertilization of, 538
formation of embryo of, 539
germination of microspores and development of male gametophyte of, 533
lambertiana, 529
laricio, 532, *536
life history of, 526
megasporangium and megaspores of, *530
megasporophylls of, 528, *529, *530, *533
microsporophylls of, 528, *532
microsporangium and microspores of, *532, *536
ovule of, *537
Pinus, pollination of, 534
radiata, megasporangiate strobili of, *528
seed of, *293, 540, *544
strobilus of, 526, *527, *528, *529, *531, *532
strobus, resin canals in stem of, *142
summary of principal features of life history of, 541
sylvestris, absence of root hairs in, 169
Pinus, *Zamia* and *Selaginella*, a comparison of, 544
Pistil, *235, 240
compound, *241
simple, *241
Pistillate flower, 246
Pisum sativum, pod of, *273
cell from root showing chondriosomes, tendril of, 31, 185
Pit, bordered, *104
Pitcher plants, 229, *231
Pith, 94, *96, 100
ray, 95, *96, 100
Placenta, 242
Placentation, types of, *242
Plankton, 346
Plant, association, 329
bodies, different kinds, 18
body, 17–42
body of seed plants, 19, *20
community, 329
ecology, 5
individual, 17
invasion, 330
kingdom, 12–13
classification of, 13, 14, 340–342
morphology, 5
physiology, 5
relationship, meaning of, 335
succession, 331
Plants, and animals, differences between, 2–3
classification of, 10, 338–342
green, materials absorbed by and changes which they undergo, 324
groups of, 7
naming of, 14
origin and meaning of scientific names of, 15
Plasmodesma, *48

Plasmodium, 406
Plasmolysis, 69, 70
Plasmopara cubensis, 421
viticola, *422
Plastids, kinds of, 49, 50
Platanus, bark of, 126
cross section of stem, *129
Plato, 10
Plum, leaf of, 188
flower buds of, *28
lenticels in, 128
Plumule, 283, 284, *306, *307
Pod, a kind of fruit (legume) 273, 278,
Podosphaera, a powdery mildew, 427
Polar nuclei, *236, 244, *555, *556
Pollen (grains), 240, 256, 260–264
of corn, 554, 555
development of, in wheat, 549
development, of in pine, *536
forms and markings of, *264
germination of, *263, 533, 551
of grass flowers, 256
of *Lilium*, *549
sacs, *236, *240
toxic, 262
Pollination, 257, 260–263
cross, 261, 564, 583, 586
by insects, 261
in pine, 534
self, 261, 583, 586
prevention of, 261
by wind, 260, 261, 534
Polypeptids, 397
Polypetaly, 564
Polypodium, 491–502
antheridium of, *494
dehiscence of sporangia, 505
fertilization and embryo development of, 495
gametophyte of, *492, 494
leaf of, *498
life cycle diagram of, *505, 506
life history of, 491
reduction division in, 502, *503
rhizome of, 497
root of, 497
sporangia of, 498, *499, *500
spores of, 492
Polyporus squamosus, fruiting body of, 451, *453
Pterosiphonia, 382
Polysiphonia, 382–*384, 457
life history diagram, 385
Polystichum, *491
Pome, 273, 277, *280
Poplar leaf, growth of, *183
Poppy, capsule of, *273
Populus, seed of, *293
alba, "suckers" in, 180
Porcupine grass, fruit of, *293
Pore fungi, 455
Porella, *471, 472
Poricidal, dehiscence, *273, 274
Portulaca, fleshy storage stems of, 141
Postelsia, 372, *376
Potamogeton, a water plant, 144
Potassium, 325, 326
Potato, flower and fruit of, *254
leaf of, in cross section, *191
petiole of, in cross section, *203
starch in tuber of, *286
tuber of, *147, *148
vine, petiole as tendril, 145
Potometer, *217
Poverty weed, rhizome of, 145
Powdery mildews, 425, *427
Precipitation, 314
Primary, cortex, 95, *96, *97, 97, 105, 109
endosperm nucleus, 265
meristems, 95, *98, 104
permanent tissues, 104, 105
root system, 156
roots, 153
xylem, *96
Primordial meristem, *96
Primordia, of flower parts, *237
Primordium of leaf, *96, 181
Primrose, showing heterostyly, *262
Procambium, 160
cylinder, *96
strands, 95, *96, 105, 109
Pro-embryo, of pine, *539, *540
of wheat, 554
of *Zambia*, 543
Progressive evolution, 337
Promeristem, 94
Promycelium, in smuts, 437, *444
in rusts, 441

Primula sinensis, leaf of, showing hydathode, *223
Prophase, 79
Prop roots, 32, 154, *178, *179
Propagation, by means of roots, 180
by means of stems, 142, 143
Proteases, a class of enzymes, 298
Protection, a function of leaves, 226
Protein fermentation, 397
Proteins, 218, 287
chemical nature of, 45
food stored in seeds, 285, 287
Proteoses, 397
Prothallium, 492, *493, 494
Protobasidiomycetes, 435, 440–445
Protococcus, 18, 352, 353
Protoderm, 95, *96, 160
Protonema, 475, *483
Protoplasm, of animals and plants, 4
of the cell, 43
discovery of, 58
doctrine, 58
Protoplast, 43, 48–53
Protostele, *106
Prunus, leaf of, *188
amygdalus, fruit of, *278
cerasus, flower of, *255
lenticels of, 128
Psalliota, spore discharge in, *444, *451, *452
Pseudomonas radicicola, 401
Pseudopodium, 406, *485
Pseudotsuga, 526
Pteridophyta, 13, 389–521
Pteris aquilina, 509
Puccinia asparagi, 444
graminis, 440, 441–445
triticina, method of infection in, *446
Puff balls, *455
Pumpkin, imperfect flowers of, *248, *249
stoma of, *196
Pure line of Gypsy wheat, *588
of Defiance wheat, *589
Pure science, 4
Pure substances, 9
Purslane, fleshy storage stems, 141
Putrefaction, 397
Pycniospore, 443
Pyrenoid, *361
Pyronema, 424
Pyrus, adventitious roots from stem cuttings, 154

Q

Quack-grass, rhizomet of, 11, *146
Quadrant stage in development of embryo, 495
Quarter-sawed wood, 119
Quercus, acorn of, *281
bark of, 126
leaf of, *188
mixed buds of, 28
rubra, sections of wood, *122
suber, 83
Quinine, an alkaloid, 219

R

Raceme, *258
Rachilla, 255
Rachis, 189
of fern leaf, 498
of grass spikelet, *247, 255, *256
Rachis, of leaf, 189
Radial symmetry, 250
Radicle, 283, 285
Radish, storage root of, 21
Rafflesia arnoldii, 31
Ramalina, 433
Raphanus sativus, storage root of, 21
Raphe, *284, *289
Raphies, *55
Raspberry, aggregate fruit of, 274, *275
mixed buds of, 28
Rate of water movement in the soil, 175
Ray flowers, *256
phloem, 110
pith, 95, 100
wood, 94
xylem, 110
Reaction, 36
chemical, 44
Receptacle, definition, of, *235, *236
of *Marchantia*, *468, *469
Recessive characters, 583
Red, algae 382–385
Sea, alga causing color of, 347
"snow" (*Sphaerella*, an alga), 18
spore stage of *Puccinia graminis*, 441, *442

Reduction division, in algae, 388
in angiosperms, *549, *551
in *Fucus*, 381
in *Funaria*, 481
in *Oedogonium*, 365
in *Pinus*, 533
in *Polypodium*, 502, *503
in *Polysiphonia*, 385
in *Riccia*, 463
in *Selaginella*, 516
in *Spirogyra*, *360
Redwood. See *Sequoia sempervirens*
Region of elongation in roots, 158
of maturation in roots, 159
of root hairs, 159
Regional successions, 331
Regular flower, *246, 250
Reindeer "moss," a lichen, 432
Relation of plants to environment, 309–331
Relationships of plants, meaning of, 335
Relative humidity, 315
Reproduction, asexual, 260, 344
by flower, 180
by gemmae, *467, 468
by roots, 180
sexual, 260, 344
by spores, 344
by stems, 142
in Thallophytes, a summary of methods, 345–346
Reproductive activities, 17, 323
functions, 19
Resin, 141, 219
Resin duct, *142
Respiration, 17
apparatus to demonstrate evolution of carbon dioxide, *299
of germinating seeds, apparatus for demonstrating heat of, *301
in leaves, 226
and photosynthesis contrasted, 73–75
and seed germination, 300
of seeds, loss in dry weight during, 300
"Retting" of flax, 396
Rhizoids, of *Anthoceros*, *471
of *Bryophyta*, 458
of *Equisetum*, *513
of *Marchantia*, *466, *467, *468, *469
of *Polypodium*, *492, *493, 494, *496
Rhizoids, of *Riccia*, *448
of *Selaginella*, *515, *517
of *Vaucheria*, *368
Rhizophores, 515
Rhizome, 21, *145
of *Equisetum*, *510
of *Iris*, *145
of *Polypodium*, *491, 497
of quack grass, *146
Rhizopus nigricans, *415–*419
Rhodophyceae, 382–385
alternation of generations in, 383
distribution of, 382
reproduction in, 383
Ribes, fruit buds of, 27
Riccia, 459–467
antheridium of, *461
fertilization, 461
fluitans, 459
gametangia of, *460, *461
gametophyte of, *459, *460, *461, *464
germination of spores, 464
life cycle, 464, *465
sporophyte, *463
successive early stages in development of, *463
spore formation, 463
Ricciocarpus natans, 459
Richardia, flower stalk of showing tissue tensions, *127
Ricinus communis, seed of, *288, *289
stages in germination of seed of, *307
development of vessel segment in, 103
Ring, on stipe of mushrooms, 451, *452
Ringing, of stems, effect on food conduction, 139
Robinia pseudacacia, stipular spines of, 186, *227
suckers in, 180
tyloses in, *126
Root, 19
anatomy of, 160
of banyan, *179
of barley, in sections, *158, *161
branching, 165
cap, 157, *167
cross section of *Alnus*, *164
clustered, of *Dahlia*, *180
diagram of, showing stages in secondary increase in thickness, *163

Root, of dicotyledon, *159
hair zone, 167
hairs, 165, *168, *169
origin of branch, *165, *166, *167
pressure, *136, 137
regions of, 157
structure of, 157
tip, 157, 159
young, diagram showing principal regions, *167
Roots, 153–180
anchorage by, 179
and stems, differences between, 153
conduction by, 178
external features of, 157
functions of, 21, 169
growth in diameter of, 162, *163
kinds of, 153
prop, *178, *179
reproduction by, 180
secondary increase in thickness of, 162, *163, 164
storage, *180
Rootstock, 21, *145
of *Iris*, *145
of *Polypodium*, *491, 497
Root system, extent of, 176
form of, 156
kinds of, 154, *155, *156
types of, 176
Rosette, 41
Rosin weed, 142
Rubus, aggregate fruit of, *275
mixed bud of, 28
weed, 142
Rudimentary embryos, 304
Rumex, cell from leaf-stalk showing crystals, *55
Runner, 21, 149, *150
Ruscus, flattened green stems (cladoes) of, 152
Russian thistle, water storage leaves of, 228
Rust fungi, 440–445
Rye, cross section of stem of, *133

S

Saccharomyces, 430, *431
Salvinia, *507
Salicornia (glasswort), fleshy storage stems of, 141
Salsola, water storage leaves of, 228
Samara, *273, 274, 281
Sambucus, lenticels in, *128
Sand-binding plant, *178
Sap, causes of ascent of, 136
nuclear, 49
path of movement, 135
Saprolegnia, *411, *412
antheridium of, *412
asexual reproduction, *411
oogonium of, *412
plant body, 411
sexual reproduction, *412
sporangia, *411
Saprolegniales, 410
Saprophyte, definition of, 391
Sapwood, *94, *113, 119
Sarcina, *393
Sarcode, 58
Sarcodes, 524
Sargasso Sea, 372, 376
Sargassum, 372, *377
Sarracenia, 229, *231
"Scarifying" of seeds, 305
Scalariform conjugation in *Spirogyra*, *358
Scale leaves, 32
Scarlet runner bean, example of liana, 24
Scenedesmus, 352, *352
Schizocarp, 274, 282
Schizomycetes, 392
Schleiden, 57, *59
Schultze, Max, 58, *61
Schwann, Theodor, 57, *60
Science, 1–5
Scion, 143, *144
Sclerotinia, 423, 424–425
Sclerotium, 425
Scouring rush (*Equisetum*), 510
Scotch broom, leaves of, 223
Scutellum, *87, 291, 308
Sea palm, a kelp, *376
fig, water storage leaves of, *228
lettuce, 357
Secale cereale, cross section of stem of, *133
Secondary growth, 106
meristems, 110

Secondary roots, 153
Secretions in plants, 219
Sections, three kinds of, *93
Sedum acre, flower of, *246
water storage leaves of, 228
Seeds, and seed germination, 295
age of, 304
adaptations favoring dispersal by, 282–308
bean, stages in germination of, *306
castor-oil plant, stages in germination of, *307
coats, 265, 283, 284
condition necessary for germination of, 295
conditions affecting vitality of, 303
development of, *199, 282, 283
dormancy, 304
and fruits, dissemination of, 292, *293
of grass, 290
kinds of food stored in, 285
maturity, 303
of monocotyledonous, with endosperm, 290
of *Pinus*, 540, *544
principal steps in development of, 260
processes going on during germination of, 297
structure of, 283, *284
testing, 304
of wheat, 559
Seedless fruits, 269, *270
Seedling, 305–308
infection in smuts, 437
Seeds and fruits, common types of, 288
distributed by man, 294
uses of, 282
Segregation, 587
Selaginella, 514, 515
development of spores of, 516
embryo of, *517, *518
female gametophyte of, *517
life history of, 515
male gametophyte of, *516
self-pollination, 261
significant points in life history of, 520
sporophyte of, 515
strobilus and sporangia of, 515
summary of life history of, 519
Selaginella, transfer of microspores and fertilization of, 518
Zamia and *Pinus*, a comparison, 544
Semi-cells, in desmids, *362
Semi-permeable membranes, 50, *64, *67
Sensitive fern, 507
Sepals, *235, 239
Septicidal dehiscence, *273, 274
Sequoia, 526
gigantea, Wawona tunnel tree, *125
cross section of trunk, *114
sempervirens (redwood) forest of, frontispiece
cross section of log of, 113
Sessile, leaf, *183
Seta, of *Marchantia*, 469, *470
of moss, *480, *481
Sex, origin and evolution of, 386–388
Sexual reproduction, definition of, 344
Shade plants, 312, 313
"Shaggy mane," a mushroom, 455
Sheath, of grass leaf, *189
Shepherdia, epidermal hairs, 197
Shepherd's purse (Capsella), epidermal hairs of, *198
origin and development of flower parts, *237
rosette in, 41
stages in development of embryo, *266
Shoot, 19, 70
climbing, 23
deliquescent, type, *22, 24
erect, 23
excurrent type, *22, 24
general external features of, 23
prostrate, 23
and root systems, balance between, 21
Shrub, 24
Sierran snow plant, 524
Sieve tubes, *85, 86, *97, *99, 101, *108
plate, *85, 86, *97
Sigillaria, 514
Silicon, 327
Silique, 273, 274, 279
Silphium, 142
Silver leaf poplar, "suckers" in, 180
Simple fruits, 272, 274
leaf, 186
Sinigrin, a glucoside, 219
Sinuses, of leaves, 186

Siphonostele, *96, 105, *106
Smilacina, rootstock of, 21
Smut, barley, *440
  corn, *436, 437
  fungi, 436–440
  losses from, 436
Sodium, a chemical element found in plants, 327
Soil, air in, 319
  conditions as affecting rate of transpiration, 222, 223
  fertility, bacteria in relation to, 229
  solutes, quantity and nature of, 309, 321
  solution, concentration and composition of, 176
  temperature, 309, 320
  water, temperature of, 175
Sol, 47
Solanum dulcamara (bitter sweet), a liana, 24
  jasminoides, petioles as tendrils, 229
  tuberosum, flower of, *254
    fruit of, *254
  leaf of, in cross section, *191
  petiole of, in cross section, *203
  starch grains of, *286
  tuber of, 21, *147
Solomon's Seal, rootstock of, 21
Solute, 46, 62
Solution, 46, 61
  colloidal, 46
  concentration of, footnote, 64, 65
  true, 45
Solvent, 46, 62
  passage of through membranes, 63
Soredium, 423, *434
Sorghum halpense, rhizome of, 145
Sorus, of fern, *498, 499, *508
  of rust, 440
Spanish bayonet, *318
Spartium, leaves of, 233
"Spawn," 450
Special creation, theory of, 11, 336
Species, 3, 12
Spectra, absorption, 209, *210, 211
Spectrum, effectiveness of different parts of, 211
Sperm, definition of, 345
Sperm, nuclei, *263, 264
  in red algae, 383
Spermagonial stage of *Puccinia graminis*, *442, 443
Spermagonium, 443
Spermatia, 443
Spermatophyta, 13, 522–570
  chief distinguishing characteristics of, 523–526
  classes of, 525
Sphaerella nivalis, 18
Sphaerotheca, 427
Sphagnum, *484–486
Spiderwort, cell from stem of, showing raphides, *55
Spike, 255, 258, 259
Spikelet, *247, 255, *256
Spindle, nuclear, 77, *78
Spines, leaf, *227
  protection by, 227
  stipular, *227
Spiral tracheal tubes, *84, 85, 102, *132
Spiral tracheids, 85
Spireme, 77, *78
Spirillum form of bacteria, 393, *394
Spirochaete, *394
Spirogyra, 352, 357–360
  germinating zygospore of, *360
  lateral conjugation in, *359
  reduction division in, *360
  reproduction in, *357
  sclariform conjugation in, *358
Spongy parenchyma, *190, *191, *200
Sporangiophore, *416, *417
Sporangium, definition of, 344
  of *Equisetum*, 510, *511
  of *Polypodium*, 498, *499
  or *Rhizopus*, *416, *417, *418
Spores of *Albugo*, *413
  asexual reproduction by, 344
  of *Cyanophyceae*, *350
  discharge of, in *Basidiomycetes*, *444
  formation of, in bacteria, 394
    in *Funaria*, 480
    in *Riccia*, 463
  forms of, in *Puccinia graminis*, 443–444
  germination of, in bacteria, 395
    in *Riccia*, 464
  of gill fungi, 450, 451

Spores of *Mycomycetes*, *409
of *Polypodium*, 492
of *Rhizopus*, *418
of *Riccia*, 463
of smut, *436
See Zoospores, Conidiospores, Oospores, Zygospores, Basidiospores, Ascospores, Chlamydospores, Uredospores, Teleutospores, Pycniospores, Microspores, Megaspores and Pollen
Sporelings of fern, *496
Sporidium, 436, 437, 441, *442
Sporocarps of water ferns, 509
Sporophylls, of *Equisetum*, *511
of *Pinus*, 526, 528
of *Polypodium*, 499
of *Selaginella*, 515
of *Triticum* (wheat), *548, 549, 550
Sporophyte, of *Anthoceros*, *471, *473
of *Bryophyta*, 458
of *Equisetum*, 512, *513
of *Funaria*, *474, *479
of *Hepaticae*, 458
of *Marchantia*, 469, *470
of *Pinus*, 526
of *Polypodium*, 497
of *Riccia*, *463, *464
of *Selaginella*, 515
of *Sphagnum*, *485
of *Triticum* (wheat), 554
Spring wood, 111, *117
Spruces (*Picea*), 526
Spurges (*Euphorbia*), stipular spines of, 186
storage in stems of, 141
as plants with latex, 142
Squash (*Cucurbita*), epidermal hairs of, 197
sieve tube and companion cells from, *85
tendrils of, 36
Squirting cucumber (*Ecballium*), fruit of, *294
St. Hilaire, theory of, 577
Stalk, cell in pine, 536, *538
cell in *Fucus*, 380
of fern sporangium, *498
Stamens (microsporophylls), *235, *237, *240, *246, *247, 250, 253, 256, 549
Stamens, union of (synandry), 252
Staminate, flower, 246
strobili of pine, 526, 528–*530
Staphylococcus, *393
Starch, 45
assimilation, 55
digestion of by diastase, *297
a food stored in seeds, 285, *286
grains, inclusions, *52, 55–56
grains from different seeds, *286
reserve, 55
sheath, *98
storage in cell, *51, *52
Stearin (a fat), 45
Stele, 96, 105, *106
of root, 160
Stem, 87–151
of alfalfa, *131
of basswood, *124
of cotton wood, external view of, *26
cross section of typical dicotyledonous, showing primary and secondary growth, *96, *109
diagram of, showing cross section of corn, *132
diagram showing longitudinal and cross section of a 10-year-old, *115
diagram of typical conifer, *120
diagram of typical hardwood, *118
functions of, 135–145
grafting, *144
modifications, *145–152
of monocotyledon, characteristic features of, 128, 131
origin, of, 881
of pear in cross section showing location of starch, *140
and root, principal distinctions between, 19
of rye in cross section, *133
storage in, 141
structure of growing point, 94
tendrils, 150
tissues derived from primary meristems, *98
woody dicotyledon-gymnosperm, secondary growth in, 106
Stems, anatomy of at nodes, 34
dicotyledonous, types of, *129
growth and development of, 88

Stems, growth medium of, 144
monocotyledonous, characteristic features of, 131
and roots, different kinds of, 31
differences between, 153
structure of, 90
types of, *129, *130
woody, general external characters of, 23
Stemonites, 406, *407
Sterigma, 435, 441
Stigma, *235, *240, 241
Stigmatic fluid, 241, 263
Stimulus, 36
Stink horns, 456
Stinking smut of wheat, *437, *438
Stipa, of fern leaf, 498
of kelps, 374
Stipe, in *Fucus*, 377
Stipular spines of black locust, *227
Stipule scar, *30
Stipules, of pea, *185, 186
of pear leaf, *188
Stock, 143, *144
Stolon, of *Rhizopus*, *416
of strawberry, *150
Stomata, *192–197
average number per square millimeter, 201, 224
control of, by guard cells, 194
depressed, of *Hakea*, *195
diagram of, *194, *196
of pumpkins, *196
raised, of *Nipa fruticans*, *195
Stone cells, *24
Stone crop, flower of, *246
water storage leaves of, 228
Storage, of food, 135
in roots, 180
in seeds, of food, 285
in stems, 141
of seeds, 303
of water in leaves, 228
Strasburger, 59
Strawberry, aggregate fruit, 274, *276
flower of, *251
runner of, 21, *150
Streptococcus, *393
Strobilus, of *Equisetum*, *510, 511, 512
Strobilus, of *Pinus*, 526–*532
of *Selaginella*, 515
Struggle for existence, 580
Style, *235, *240, 241
Suberin, 83
Successions, plant, 331
"Suckers," 180
Sucrose (cane sugar), 45, 398
Sugar beet, storage in, 21
tap root system of, *154
Sugars, 45
as stored food in seeds, 285, 286
Sulphur, 325, 327
Summer wood, 111, *117
Sun plants, 312, 313
Sundew, leaf of, 229, *231
Superior ovary, *253, *254
Support, a function of stems, 135
Suspensor, cell in wheat embryo, 558
cells in pine, 539, *540, *544
of *Rhizopus*, *419
of *Selaginella*, 514, *517, *518
of *Zamia*, 543
Sweet clover, tap root system of, *155
Sweet pea (*Lathyrus odoratus*), flower of, *250
tendril of, 31, 229
Sweet potato, storage root of, 21
Symbiosis, 401
of *Cyanophyceae*, 348
of alga and fungus in lichens, 432
Symbiotic bacteria, nitrogen fixation by, 401
Symmetry of flower, 250, 251
Sympetalae, 252
Sympetaly, 251, *252, 564
Synandry, 251, *252, *253
Synapsis, 502
Synconium, 275
Synechococcus, *348
Synergids, *236, 244, *245, *555, *556
and antipodal nuclei, fate of, 265
Synsepaly, 251, 252
Systematic botany, 4, 5

T

Taeniophyllum, 232
Tannins, 141, 142
plant secretions, 219
Tapetum, *500, *546, *547

Tap root system, *154, *155, *156
Taraxacum, fruit of, *293
latex tubes in the root of, *143
rosette in, 41
Tarweed, secretions from glandular hairs, 197
Tassel (staminate inflorescence), of corn, 248
Taxonomy, 5
Tegmen, a seed coat, 284
Telophase, 79
Teleutosorus, 441, *442
Teleutospore, 441, *442, *444
Temperature, and seed germination, 296
a factor influencing rate of photosynthesis, 216
soil, 309, 320
of air and transpiration rate, 223
Tendrils, leaf, 229
stem, 150
of sweet pea, 31
Terminal bud, 26
scar, 30
Testa, a seed coat, 284
Testing of seed, 304
Tetrads of spores in *Bryophyta*, *Pteridophyta* and *Spermatophyta*, 459, *465, 481, *483
in *Funaria*, 484
in *Pinus*, 533, *536
in *Polypodium*, *505
in *Riccia*, *464, *465
Tetraspores, of red algae, 383, *384
Thallophytes, 13, 343–406
autophytic, 346
characteristics of, 343
heterophytic, 346
methods of reproduction in, 343, 345, 346
subdivisions of, 346
Thallus, 343, 459, 467
Thein, an alkaloid, 219
Theophrastus, 10
Theories as to origin of species, 577
Theory, of constancy of species, 11
of evolution, 3
of organic evolution, 336
of special creation, 11, 336
Thermotropism, 36
Thiospirillum, *394
Thigmotropism, 36
Tilia, diagram of three-year-old stem of, *124
Tillandsia, 525
Tillering, in cereals, *88
Tilletia, *437, *438
Timothy, ligule of leaf of, 189
Tissue, collemchyma, *82, 83
conducting, *84, *85
cork, *81, 83
definition of, 18, 80
epidermal, *81
mechanical, *83
meristematic, 80
origin and development of stem, 94
parenchyma, 80, 81
tensions, in flower stalk of calla lily, *127
Tobacco, secretion from glandular hairs, 198
Tomato, cell from flesh of fruit showing chromoplasts, *52
Tooth fungi, 455
Torus, 104
Tracheae, 102
Tracheal tubes, *99, 102
different kinds of, *84, 85, 102, *132
origin of, *101, *103
Tracheids, *48, *84, 85, *99, 102, 103
different kinds of, *84, 85
in leaf, *200
Tradescantia, cells from stamen hairs, *46
cell from stem, showing raphides, *55
Transformations of materials and energy, 323
Transmission, of stimuli, 36
Transpiration, 17, 21, 172, 219–225
conditions affecting rate of, 222
cuticular, 224
means of reducing, 223, 225
potometer for measuring rate of, *217
pull and water cohesion, 135
rate of, 177, 222
regulation of, by action of guard cells, 225
stomal, 224
and transpiration stream, 138, 220
utility to plant, 220
Trees, 24, *74, *75, *84
felled, determining age of, 115

Trees, branching of, *24
in winter condition, 30
Trentepohlia, 352
Trichodesmium erythraceum, 347
Trichogyne, 383, *384
Trifolium, seedling of, *170
Triticum. See also Wheat
grain of, in lengthwise section, *284
life history of, 547
spikelet of, *256
starch grains of, *286
Tropaeolum, petiole as tendril, 229
Tropisms, 32–39
Tube-nucleus, *263, *538
Tuber, 21, *147, *148
Tulip tree, stipules of, 186
Tumboa, 544
Turgor, 174
Turgor pressure, 68
Turnip, storage root of, 21
Tyloses, *126

U

Ulmus, bark of, 126
fruit of, *293
Ulothrix, 352, 354, *355, 357
Ulva, 18, 357
Umbel, 258, *259
Uncinula, 427
Uredosori, 441, *442
Uredospore, 441, *442
Use and disuse, Lamarck's theory of, as to origin of species, 578
Usnea, 432
Ustilago avenae, *439
levis, *439
maydis, *436, 437
Utricularia, 31, 229, *232

V

Vaccinium, flower of, *252
Vacuole, *49, 54
Valves, of diatoms, 370, *371
Variation, bud, *578
heredity and, 571
in pinnae of fern, *575
Variations, continuous or fluctuating, 580
kinds of, 575
Vascular bundle, 95
cross section of young, in dicotyledonous stem, *99
Vascular bundle, cross section of corn, *132
of leaf, 202, *203
Vascular cambium, 93, 106
Vascular tissue, 100
Vaucheria, 352, 367–369
zoospore formation in, 367, *368
Vegetable ivory, 282
Vegetative activities, 17
functions, 19
nuclei, *536
and reproductive functions, 234
Veining of leaves, *187
Veins of leaf, 186, *202
Venation, 186, *187
Venter of archegonium, of *Equisetum*, *513
of *Funaria*, *478
of *Polypodium*, 494
of *Riccia*, 461, *462
of *Selaginella*, 518
of *Sphagnum*, *485
Ventral canal cells, 461, *462, *538
Venus' fly trap, an insectivorous plant, 229, *230
Verbascum, epidermal hairs, 197
Vestibule, *193, *195
Vibrio cholerae, *394
Vicia faba, flower of, *250
primary root of, *162
root system showing geotropic curvature, *33, *34
Viola, capsule of, *273
net veining in leaf of, *187
Violet, capsule of, *273
net veining in leaf of, *187
Virginia creeper, air roots of, 32
Viscum, 524
Vitality of seeds, conditions affecting, 303
Vitis, a liana, 24
mixed bud of, 28
tendrils of, 36
Volva, *449, 451
Von Mohl, Hugo, 58

W

Walnut, fruit buds of, 27
leaf of, *188
Wandering Jew, plasmolysis of epidermal cells of, *69

Water, absorption of, 169, 171
absorption and seed germination, 297
available in soil, 173
factor, affecting intake of from soil, 173
a factor, in seed and fruit dissemination, 292
factors affecting, available in soil, 317
"felt," 367
ferns, 507, 509
forms of, in soil, 172
functions of, in a plant, 171
importance of, in life of plant, 169
lily, *321
mold, 411, *412
movement, rate of, in soil, 175
role of, in germination of seeds, 295
storage by leaves, 227
tissue, 228
weed, 525
Wawona tunnel tree, *125
Wheat, development of anther of, *546
development of embryo sporophyte of, 554
development of endosperm of, 556
diagram of life cycle, *561
embryos of, 558, 559
female gametophyte (embryo sac) of, 552
stages in development of, 552
fertilization of, 553
fibrous root system of, *155
grain of, in lengthwise section, *284
grain in cross section, *290
life history of, 547
longitudinal section of anther, *547
longitudinal section of embryo, *87
male gametophyte of, 551
stages in development of, 551, *553
megasporophylls and megasporangia, 550
microsporophylls and microsporangia, 549
pollination and development of the pollen tube of, 553
seed of, 559
seedling of, showing root hairs, *168
spikelet of, *256
stages in germination of, 302, 308
summary of principal features in life history of, 560
White clover, seedling of showing root hairs, *170
White pine blister rust, *447, *448
White rust of crucifers, *413, *414
Whorled buds, 27
Wild cucumber, fruit of, *273
Wilting coefficient, 173, 174
Wilting, permanent, 173
Wind, an environmental factor, 309, 316, 317
a factor in seed and fruit dissemination, 292
Wind timber, *316
Wings, of pea flower, *250
Winter killing, 175
Winter twig of cottonwood, *26, *30
Wolffia, 31
Wood, 93, 102
grain of, 119
of hard maple in section, *121
parenchyma, 102, 104
of pine, showing structure of, *117
of red oak, *122
of redwood in sections, *113, *114
rays, 94
sections of, *121
sorrel, leaf of, *188

X

Xanthium, root of, *293
Xanthophyll, 50, 352
Xerophytes, *318, 319
Xylem, 95, *96, *98, *99, 102, 105, *109, *112
ray, 110

Y

Yeast, 430–*431
Yucca, monocotyledon with cambium ring, 130
a xerophytic plant, *318

Z

Zamia, 542–545
Selaginella and *Pinus*, a comparison, 544

Zea mays, cross section of stem, *132
cross section of vascular bundle, *132
embryo sac, development of, *555
grain of, *281
pollen tube of, *554, *556
prop roots of, 154, *178
starch grains of, *286
Zebrina pendula, plasmolysis of epidermal cells of, *69
Zinc, 327
Zoology, 2
Zoospore, definition of, 344
Zostera, 525
Zygomycetes, 410
Zygomorphy, 564
Zygospore, definition of, 345
in *Ulothrix*, 354, *355
Zygote, 265, 295, 344
Zymase (sugar-fermenting enzyme), 398, 431

Polypodium
vulgare
Phegopteris
polypodioides
hexagonoptera
dryopteris (oak)
Adiantum
pedatum
capillus veneris
Pteris
aquilina
Pellaea
atropurpurea
(Woodwardia)
Asplenium
trichomanes
ebeneum
ruta-muraria
acrostichoides
filix-femina
Camptosorus
rhizophyllus
Polystichum
acrostichoides (C)
(lonchitis (holly)
Aspidium
thelypteris (marsh)
simulatum
noveboracense
marginale
Goldianum
cristatum
spinulosum - intermedium
Cystopteris
bulbifera

Dicksonia
punctilobula
Onoclea
sensibilis
struthiopteris
Osmunda
regalis
claytoniana
cinnamomea
Botrychium
lanceolatum
matricariaefolium
ternatum
{obliquum
{dissectum
virginianum